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PLANT COMMUNITIES IN THE MARSHLANDS OF SOUTHEASTERN LOUISIANA

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PLANT COMMUNITIES IN THE MARSHLANDS OF SOUTHEASTERN LOUISIANA

INTRODUCTION

The marshlands of Louisiana include large interrupted areas of fresh water marsh and a vast, practically unbroken expanse of brackish and salt-water marsh along the coast. This saline "wet prairie" forms a part of the still greater body of marsh vegetation which extends from Maine to Texas. Since Louisiana includes over four million acres of marshlands we resolved to inspect a considerable number of marsh areas in the southern part of the state and to conduct routine monthly studies on marsh habitats within a day's journey from New Orleans.

This study has involved 23 reconnaissance trips, 66 monthly visits to seven transects made during one annual cycle, and about twenty confirmatory trips subsequent to the routine investigation. On each trip we noted, so far as possible, the relative abundance and phenology of each species in every community of the transect visited. Of the habitat factors we determined water level, salinity of surface water and soil water, and also the water content and organic matter in the upper 2 feet of soil. Although our quantitative data were obtained only from marshlands in the vicinity of New Orleans we believe that they represent in a general way conditions throughout the Gulf Coastal Plain. The work has now been in progress for more than 4 years. During that time we have had the loyal co-operation of numerous assistants in the departments of Botany and Zoology of Tulane University, and we gratefully recognize their valuable contributions to the study.

HISTORICAL

As early as 1903 Ganong described the salt marshes of the Bay of Fundy and the effects of dikes on the marsh vegetation. An interesting account of the New Jersey marshes was given by Smith in 1907. He divided the salt marshes into those that are covered by each high tide, those covered only by the highest tides and those which are rarely covered by any except the most extreme storm tides. He briefly indicated the succession of the important species, gave a meager account of the edaphic factors, and discussed the economics of the marshes. In addition he showed that the marshes degrade and sink if the salt water is excluded and advised ditching to the sea as a method of marsh improvement and mosquito control. A more complete description of the vegetation of the salt marshes of New Jersey was given by Harshberger (1909). In this paper the author also discussed the transition from fresh water to brackish water marshes and made an attempt at correlating the distribution of salt marsh vegetation with the salinity of soil water.

Johnson and York (1915) described the littoral vegetation at Cold Spring Harbor and correlated vegetation with substratum, currents, tides, and salinity. They suggested that, in any region, the vertical range of a littoral plant would be exactly proportional to the range of the tide. In the New Jersey marshes the formation of salt marsh pools, from a few feet across to an acre or more in extent, is fairly common (Harshberger, 1916). These pools were shown to be due to the rapid decay of both aerial and subterranean parts of vegetation which is covered by tide-carried rafts of vegetable débris. The problem of bank softening and soil shrinkage due to exclusion of salt water was further elaborated by Rudolphs (1926). He also showed that bald spots in the marshes were due to excessive salinity (up to 22.2 percent salt) and that these spots revegetated very slowly. Emphasis was placed on the saline hydroperiod as a major factor in the delimitation of salt marsh communities in North Carolina by Wells (1928). He also listed the important species in each community and indicated their successional relations.

Of the studies in the Gulf Coastal States the early work of Mohr (1901) is significant. In it he described the relatively fresh water marshes of the Mobile River estuary and the littoral marshes of the coast which he designated as the "southern juncaceous formation." Lowe (1919, 1921) discussed the geology and soils of the Mississippi marshes, especially of Pascagoula and Mobile bays, and listed the predominant marsh species. In the South Atlantic and Gulf States there are 5,600,000 acres of salt marshes and of this area 3,381,500 acres are located in Louisiana (Griffitts, 1928). Louisiana has the doubtful honor of having nearly twelve times as much salt marsh as New Jersey and almost half the total salt marsh area of the Atlantic and Gulf coasts.

In his work on the fur animals of Louisiana Arthur (1931) included much that is of value to the plant ecologist. He indicated the beneficial effect of humus and the harmful effects of drought and fire on muskrat production in the Louisiana marshes. Viosca (1928) in discussing the physiography of the Louisiana wetlands indicates that of the total area of Louisiana nearly one-third (10,000,000 acres) is given over to swamps, marshes, or open water. He includes a good discussion of the biotic interrelations in the marshes and makes an impassioned plea for the restoration of natural conditions which are best suited to an abundant marsh flora and fauna. In a discussion of the vegetation of Cat Island, Mississippi, Penfound and O'Neill (1933) described the communities of both fresh and brackish water marshes, and indicated their successional relations. They also gave physical data which, though meager, suggested that the water table and the salinity of the soil were of the utmost importance in the delimitation and composition of marsh communities.

Of the investigations of the salt deserts of the western United States

those of Kearney (1914) and Flowers (1934) are outstanding. In his study of the vegetation of Tooele Valley, Utah, Kearney described the salt flat communities, indicated their successional relations and their dependence on salinity and soil moisture. In both of the above investigations the marshes, as described, are very different from those of the Atlantic and Gulf coasts. In fact, Flowers lists only eleven spermatophytes common to the Great Salt Lake marshes and the salt marshes of Louisiana. Of the salt marsh species salt grass (*Distichlis spicata*[1]), is classed by him as the most versatile, successful and salt tolerant plant of the region. In both investigations salinity determinations were based on the dry weight of the soil. In spite of this fact Flowers states that "the real feature of significance is the concentration of the soil solution." Since we have determined only the salinity of the surface water and that of the soil solution no comparisons are possible between their data and our results in the Louisiana marshes.

Several of the more recent papers on marshes have dealt with salinity relations. Alexander et al (1932) showed that the salinity of the soil water was usually higher and fluctuated less than that of the surface water in the estuary of the Tees River. Nicol (1935) confirmed these results and demonstrated that the interchange of salt between mucky soils of pools and the superposed surface water was very slow. It was pointed out by Steiner (1934) that the osmotic pressure of the soil solution of the marsh soils decreased with depth to a point about 12 to 15 inches below the soil surface. Since the root level of marsh plants was also found by him to vary with the species it is evident that autecological studies are necessary in order to understand the water economy of halophytic plants. These and other problems concerning halophytes are summarized by Chapman (1936).

CLIMATE

The areas under investigation are all situated within 70 miles of New Orleans in southeastern Louisiana. The New Orleans area possesses an essentially semi-tropical and coastal climate because of its latitude (30° North) and its proximity to the Mississippi River, to Lakes Pontchartrain, Borgne, and Salvador, and to the Gulf of Mexico. The nature of the climate is indicated by the data in Table 1, which are taken from the reports of the

TABLE 1. GENERAL METEOROLOGICAL CONDITIONS, 1932, 1933, AND NORMAL (LONG TERM AVERAGE)

	Temperature mean annual	Rainfall *inches*	Relative humidity (12 M)	Sunshine *percentage*	Wind direction	Growing season
1932 ..	70 3°	72 12	61	61	Northeast	278
1933. .	72 1°	48 49	58	62	Southeast	345
Normal. ..	69 4°	59 34	63	58	Southeast	326

[1] The "Manual of the Southeastern Flora" by Small (1933) has been closely followed in nomenclature.

United States Weather Bureau, kindy furnished by the New Orleans office. The mean annual temperature is 69.4°F. with mean monthly temperatures of 54.6°F. for January and 82.4°F. for July. Precipitation is quite evenly distributed throughout the year with July and August as the wettest months and October and November as the driest. Despite the considerable annual rainfall (59.34 inches) and the high relative humidity (63 percent at 12 M.) the amount of sunshine (58 percent of possible) is not far below the average for the Mississippi valley. Since there are few severe frosts and since the frostless season is 326 days, some species are found in bloom every day of the year.

Our detailed studies on the transects were started in February, 1932, the warmest February of record and with very low rainfall (Fig. 1). It

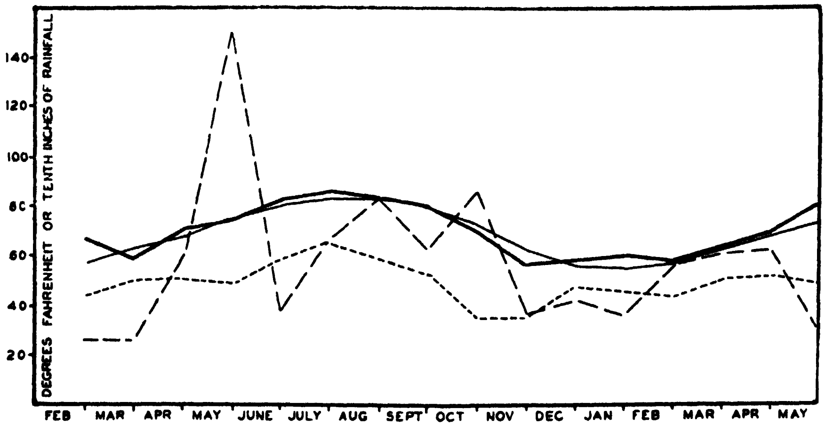

FIG. 1. Monthly temperatures (heavy solid line) and monthly rainfall (broken line) during period of investigation compared with mean monthly temperatures (light solid line) and mean monthly rainfall (dotted line).

was preceded by two months also characterized by high temperatures but with abundant rainfall. The average temperature for the year was 1.0°F. above the normal and the total rainfall for the year was 14.53 inches above the long term average, with a maximum excess of 15.06 inches in May. Despite the shorter frostless season (278 days) the weather in 1932 was very favorable to the development of vegetation as well as mosquitoes, and was generally acclaimed as an unusually bad mosquito year. The weather of the first five months of 1933 was not greatly different from the long period average. The average temperature for the same period (66.4°F.) was 2.7°F. higher than the normal (63.7°F.), but the average monthly rainfall (4.95 inches) was only 0.11 inch greater than the long term average (Fig. 1). Since other climatic conditions were typical the last five months of the period of investigation were especially favorable to the development of vegetation.

PHYSIOGRAPHIC CONDITIONS

The marshes of southeastern Louisiana include approximately one and three-quarter million acres of fresh water marsh and about two and one-half million acres of sea marsh (Viosca, 1928). The fresh water marshes occur in large interrupted areas in the interior of the state, but the salt marshes occupy a practically unbroken strip of coastline several miles in width (Fig. 2). Some of the marshes occur in or adjacent to the Gulf Coastal

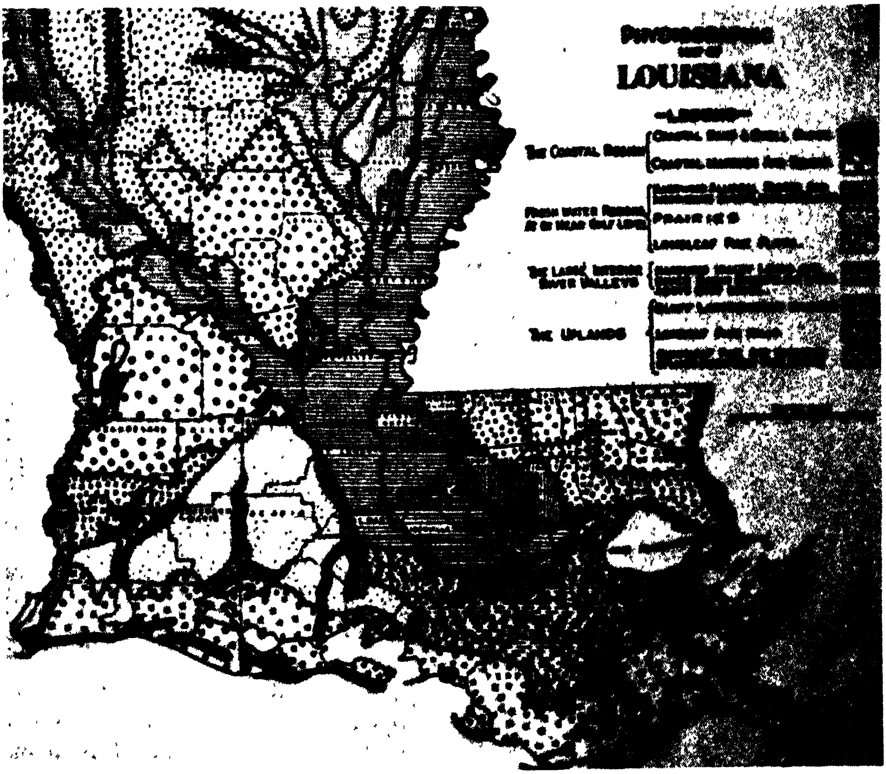

FIG. 2. Physiographic map of Louisiana.

Plain but most of the marsh area under investigation is situated in the lower Mississippi delta below Lake Pontchartrain. The sediments of the Gulf Coastal Plain are of comparatively recent marine origin and, except in the flood plains of the longer dissecting streams, are usually acid in reaction. The Mississippi delta in southeastern Louisiana is still more recent in origin but is characterized, especially near the coast, by soils which are typically alkaline in reaction.

In the Mississippi alluvial plain the river now has no tributaries below St. Francisville, and aside from the present passes at the mouth of the Mississippi there are no active distributaries except the Atchafalaya River.

But in the past there were several outlets which either have been naturally abandoned by the parent stream or closed off by levee builders. These distributaries issued from the Mississippi or the Atchafalaya, and by branching formed a fan-shaped delta of great extent (Fig. 2). The varying topography of the Mississippi alluvial plain is the result of uneven deposition of sediments by these different distributaries.

In general the region under investigation is an extensive alluvial plain with little relief which dips slightly gulfward and approximates sea level throughout the lower portion. Each deltaic stream included within this alluvial plain is flanked by natural levees, popularly called "front lands," which are formed by the deposition of the coarser sediments during flood periods. The elevation of these natural levees gradually decreases away from the stream front to the so-called "back lands" or "black lands" which differ from the front lands in the finer texture and darker color of their soils. Where the back lands dip below the mean water table they are occupied by cypress-gum swamps and marshes in fresh water areas but only by marshes in more saline areas. These wetlands do not drain into the main streams but are merely catch basins for the overflow waters and for rainfall in the alluvial plain. These catch basins are drained by sluggish, meandering bayous, characterized by insignificant levees and designated as "swamp drainage bayous" by Viosca (1933). In addition there are occasional elongated or nearly circular "islands" which vary from a few inches to several feet above the surrounding marshes. Most of these, especially in southwestern Louisiana, are former barrier beaches although others appear to be outlying fragments of the Gulf Coastal Plain. Whenever one of these elevations is clothed with evergreen oaks it is termed a *chênière*.

TRANSECT STUDIES

Location of Transects

In attempting to locate representative areas, marshes from Cat Island, Mississippi, westward to East Cote Blanche Bay, and from Lake Pontchartrain southward to Grand Isle and the Passes at the mouth of the Mississippi River were visited. The preliminary survey, involving a total of 23 trips, revealed a surprising diversity in the composition of these "wet prairies." Our plan was to include areas of varying degrees of salinity from fresh water areas to the most saline habitat, but near enough to New Orleans to permit routine investigation. We were also interested in locating marshes which were essentially untouched by man. This required a prolonged reconnaissance which necessitated some difference in time in locating proper stations. However seven transects were finally established within a radius of 70 miles from Tulane University, New Orleans (Fig. 3).

The fresh water marsh transect is situated near Raceland in the Lake Des Allemands drainage area. This transect, hereafter called the Raceland

FIG. 3. Location of transects near New Orleans.

transect, is just south of the Old Spanish Trail (U. S. 90) 36 miles southwest of New Orleans. A nearly fresh water area (less than 0.5 percent salt) known as the Slidell transect was selected near Slidell on U. S. 90 some 43 miles northeast of New Orleans, at the junction of the Pearl River delta and the Gulf Coastal Plain.

Three transects were located in brackish marsh areas (0.5-2.0 percent salt). The Bayou Villars transect (0.3-1.0 percent salt) is situated near the confluence of Bayou Villars and Bayou Barataria in the Mississippi Alluvial Plain on Louisiana Highway 30 (Fig. 3). A special feature of this transect is a swamp of bald cypress in which the trees of the forest-marsh ecotone are dwarfed and scraggly. A second brackish station known as the Oak Island transect (0.8-1.4 percent salt) was established on the northwestern border of an "island" of live oaks *(chênière)* in the Pearl River Alluvial Plain, approximately 40 miles northeast of New Orleans on U. S. Highway 90. This transect is characterized by the absence of cypress trees probably due to the relatively high salinity of the area. The third, known as the Foster transect (0.6-1.7 percent salt), is situated on Grand Bayou near the Foster Packing Plant about 45 miles south of New Orleans on Louisiana Highway 31.

The two saline stations are also located on Grand Bayou, but well toward the Gulf of Mexico (Fig. 3). The Yellow House transect was laid out in a marsh of much higher salinity (3.3-3.7 percent salt) west of Empire, some 60 miles south of New Orleans on Louisiana Highway 31. This transect was established on the western shore of Grand Bayou 1.5 miles below its confluence with Mevers Canal and approximately 8.5 miles from Empire (Fig. 3). The Popich transect (3.5-4.5 percent salt) is 3 miles south of the Yellow House transect on the eastern shore of the Bayou across from an oyster camp owned by Mr. Joseph Popich. The unique character of this transect is the presence of a honey mangrove community along the front lands of the bayou.

Methods of Investigation

Our plan was to study each of the seven transects, once a month, throughout an annual cycle. On each trip, so far as practicable, the relative abundance and phenology of each species of plant and animal in every community of the transect were noted. Of the habitat factors the writers observed the depth of the surface water (where present) and collected surface water from the marsh and water from adjacent bayous or lagoons for the determination of salinity. In addition soil samples were obtained from the first and second feet of soil by means of a soil auger for the determination of water content and percentage of organic matter (Fig. 4). After allowing the water in the hole to attain a constant level, the position of the water, with reference to the soil surface, was ascertained and a quart sample was procured for the determination of salinity. The amount of slope within each transect was determined by comparing the water levels in the various zones during periods of high water, when the transects were largely or wholly submerged.

Vegetation of the Transects

Each transect was started on an elevation and was projected across the typically gradual slope to the extensive paludal basins away from the ridge.

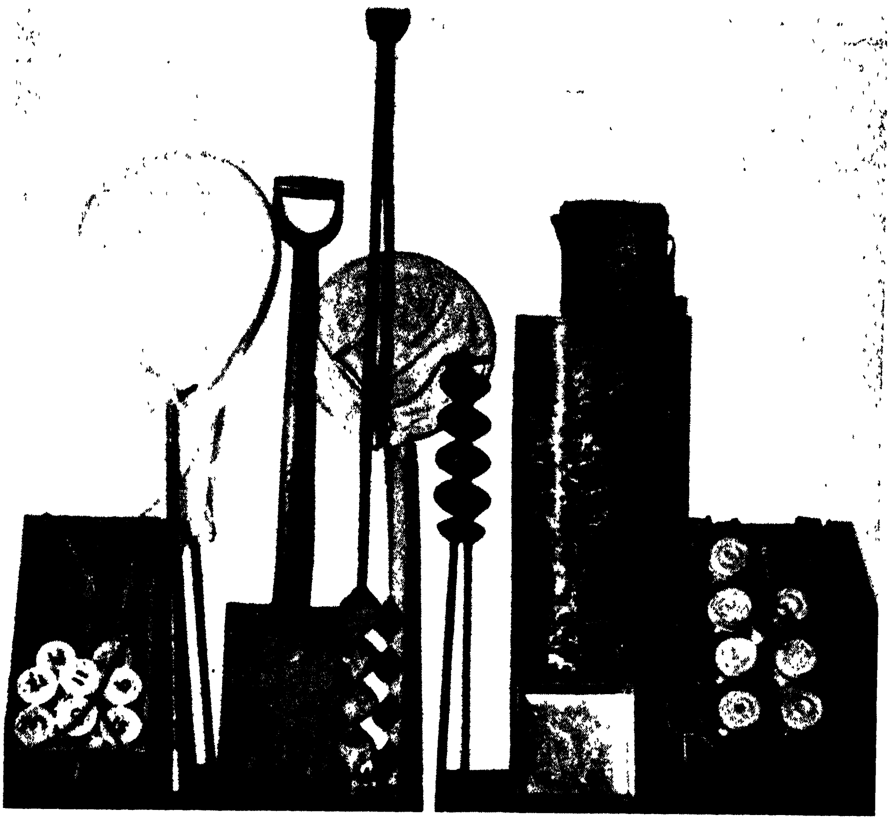

FIG. 4. Equipment utilized in marsh studies.

The elevations and a major portion of the slopes are characterized by a water level below the soil surface whereas the basins usually have standing water. In relatively fresh water areas the elevations, if of sufficient height, are occupied by pine or oak forests which are separated by a cypress-gum swamp from the marshes in the basins (Table 2). In brackish or saline areas with similar elevations the cypress-gum swamp is eliminated and the oak forest is now fringed by one or more zonal communities (where the average water level is below the soil surface) beyond which lies the usually extensive marsh (characterized by standing water). *It should be emphasized also that the transition from one community to another is conditioned by a change in elevation of as little as 3 inches since four communities may occur on a slope having a fall of less than 1 foot.*

The transects studied include 11 distinctly different communities of which three are forests, four are zonal associes and four are true marshes of considerable extent. In addition, there are several consocies which are correlated with local differences in habitat factors. Since the pine and oak

TABLE 2. FOREST, ZONAL, SWAMP, AND TRUE MARSH COMMUNITIES IN TRANSECTS

Transect	Average percent salt	Forest	Shrub	Cane	Salt grass	Swamp	True Marsh
		Average level of the water table in inches					
		– 30 to —4	—10 to —6	—6 to +1	—1 to +1	—4 to +12	+1 to +12
Raceland	0.0			.		Taxodium —Nyssa	Typha —Scirpus
Slidell	0 1 to 0 4	Pinus				Taxodium —Nyssa	Mariscus
Bayou Villars	0 3 to 1.0	Quercus	. ...	Phragmites —*Spartina cynosuroides*		Taxodium —Nyssa	Spartina —Distichlis —Juncus
Oak Island	0.1 to 1 1	Quercus	Baccharis —Iva	Phragmites —*Spartina cynosuroides*	Distichlis		Spartina —Distichlis —Juncus
Foster	1 1 to 1 5	.		Phragmites —*Spartina cynosuroides*	Distichlis		Spartina Distichlis —Juncus
Yellow House	1 4 to 3 7		Baccharis —Iva	Phragmites —*Spartina cynosuroides*	Distichlis		*Spartina alterniflora*
Popich	4.0 to 4 5			*Avicennia	Distichlis		*Spartina alterniflora*

*Avicennia, although a shrub here occupies a niche similar to that filled by the canes in other transects.

forests are not closely allied to the marshes only brief mention is given them here. But since the cypress-gum swamps frequently border directly on the marshes and are subject to similar edaphic influences they are granted rather complete discussion. In addition to the vegetational units in the transects there were five aquatic communities in fresh water areas and two others in brackish water regions.

RACELAND TRANSECT

The Raceland transect extends across a cypress-gum swamp (Taxodium-Nyssa associes), a forest border of willow and buttonbush and a fresh water marsh (Typha-Scirpus associes). Water stands almost continuously on the entire transect, the average depth in the cypress-gum swamp being nearly 8 inches, that in the marsh more than 11 inches, while in the intervening willow-shrub zone it averages nearly 12 inches in depth. The cypress-gum swamp has been cut over and is somewhat open but it includes a considerable number of large trees of bald cypress *(Taxodium distichum)* and tupelo gum *(Nyssa aquatica)* and excellent reproduction of bald cypress. Of the other trees water ash *(Fraxinus profunda)* and swamp maple *(Rufacer Drummondii)* are most abundant, with black willow *(Salix nigra)* restricted largely to the swamp border. Since the swamp is rather open there is an abundance of herbaceous species some of which are found also in the marsh (Table 3). The forest border, although including many of the cypress-gum swamp species, is characterized by a greater number of willows and buttonbushes *(Cephalanthus occidentalis)*, by an abundance of cut-grass

TABLE 3. PRESENCE AND RELATIVE ABUNDANCE OF SPECIES (SCALE 1 TO 10) IN THE CYPRESS-GUM SWAMPS (TAXODIUM-NYSSA ASSOCIES). *IMPORTANT SPECIES

SPECIES	Common Name	Raceland (0.0 percent salt)	Slidell (0.4 percent salt)	Villars (0.6 percent salt)
TREES				
**Fraxinus profunda*	Water ash	4		6
Liquidambar Styraciflua	Red gum	0.1		
**Nyssa aquatica*	Tupelo gum	3		
**Nyssa biflora*	Sour gum		4	
**Rufacer Drummondii*	Swamp maple	2	2	3
Salix nigra	Black willow	1	1	3
Tamala pubescens	Red bay			1
**Taxodium distichum*	Bald cypress	8	8	10
SHRUBS AND VINES				
Amorpha fruticosa	False indigo		0.1	
Ampelopsis arborea	Pepper-vine	0.5		1
**Baccharis halimifolia*	Buckbrush		3	8
Berchemia scandens	Supplejack	0.5		
Brunnichia cirrhosa	Florida-vine	1		4
**Cephalanthus occidentalis*	Buttonbush	4	1	2
Cerothamnus ceriferus	Wax myrtle		2	3
Convolvulus repens	Marsh bindweed		0.5	2
Ipomoea sagittata	Marsh morning-glory			2
Iva frutescens	Marsh elder		3	1
Mikania scandens	Hemp-vine	2		
Rubus louisianicus	Swamp blackberry	1		
**Sabal minor*	Dwarf palmetto		2	8
Sambucus canadensis	Elderberry	0.5		
Styrax grandifolia	Storax	0.1		
HERBS				
Achyranthes philoxeroides	Marsh-button		3	
Acnida cuspidata	Southern water-hemp			2
Ageratum conyzoides	Ageratum	0.1		
Asplenium ebenoides	Scott's spleenwort	0.1		
Aster exilis	Slim aster		0.1	
Blechnum serrulatum	Swamp fern	0.1		
Bramia Monnieri	Hedge-hyssop		8	2
Carex comosa	Bristly sedge	0.5		
Carex crus-corvi	Crowfoot sedge	1		
Carex lupulina	Hop sedge	1		1
Chaetochloa geniculata	Marsh fox-tail		0.5	
Chaetochloa magna	Giant fox-tail			0.1
Crinum americanum	String-lily		6	
Cyperus virens	Swamp sedge	1		
Dryopteris patens	Shield fern	0.5		
Dryopteris thelypteris	Marsh shield fern	0.5		
Echinochloa Walteri	Duck millet		0.1	2
Echinodorus radicans	Creeping bur-head	0.5		1
Eleocharis albida	White spike-rush			1
Eleocharis olivacea	Green spike-rush		0.5	
Erianthus saccharoides	Plume grass	1		
Globifera umbrosa	Dwarf moneywort		3	
Gratiola virginiana	Clammy hedge-hyssop		3	
Hibiscus lasiocarpus	Rose-mallow		1	3
Hygrophila lacustris	Water-willow	1		
Hymenocallis rotatum	Spider-lily		4	
Ibidium cernuum	Ladies'-tresses	0.1		
Iris virginica	Coastal plain iris		3	
Isnardia palustris	Marsh purslane	0.5	8	1
Juncus effusus	Common rush			5
Justicia lanceolata	Water-willow	3		
Kosteletzkya virginica	Salt-marsh mallow		2	4
Ludwigia glandulosa	Ludwigia	1		

TABLE 3 (Continued).

SPECIES	Common Name	Raceland (0.0 percent	Slidell (0.4 percent salt)	Villars (0.6 percent salt)
HERBS (Cont.)				
Myriophyllum pinnatum	Water-milfoil		3	
Onoclea sensibilis.	Sensitive fern	1		
Osmunda regalis	Royal fern	1	1	.
Panicum anceps	Beaked panic-grass		1	
Panicum agrostoides	Red-top panic-grass			2
Panicum gymnocarpon	Swamp panic-grass	2		2
Panicum virgatum	Feather grass		2	
Persicaria Opelousana	Smartweed	3		
Persicaria portoricensis	Giant knotweed	4		
**Persicaria punctata*	Dotted smartweed	3	1	3
Pluchea camphorata	Spicy marsh fleabane		1	0 5
Pluchea foetida	Viscid marsh fleabane		1	
Pontederia cordata	Pickerel weed	2	2	6
Proserpinaca pectinata	Mermaid-weed		0 5	
Rumex verticillatus	Swamp dock	1	1	2
Rynchospora corniculata	Horned rush	2		1
Sabbatia campanulata	Slender marsh pink		1	
Sacciolepis striata	Gibbous panic-grass		0 5	
**Sagittaria lancifolia*	Delta potato	1	2	4
Samolus floribundus	Brookweed		2	1
Saururus cernuus	Lizard's tail	1		4
Scirpus californicus	Giant bulrush			0 1
Sesban Emerus	Coffee bean			0 5
Solidago mexicana	Seaside goldenrod		1	2
Spartina patens	Couch grass			1
Tradescantia reflexa	Spiderwort	0 5	.	
Typha angustifolia	Narrowleaf cattail			2
Typha latifolia	Broadleaf cattail			3
**Zizaniopsis miliacea*	Cut grass	2	3	4
HERBS (on logs or stumps)				
Boehmeria cylindrica	False nettle	2		
Hydrocotyle verticillata	Marsh pennywort	1	0 2	1
Lycopus rubellus	Water hoarhound	4		
Mosses (several species)		1	1	
Triadenum petiolatum	St. John's-wort	2		
Trisetum pennsylvanicum	False oat	1		
AQUATICS				
Azolla caroliniana	Floating fern	2		
Ceratophyllum submersum	Coontail	0 1		
Lemna minor	Lesser duckweed	2		...
Piaropus crassipes	Water hyacinth	1		
Riccia fluitans	Dissected liverwort	0 5		
Ricciocarpus natans	Heart-shaped liverwort	0 5		
Spirodela polyrhiza	Greater duckweed	1		1
Utricularia gibba	Humped bladderwort		0 1	
Utricularia macrorhiza	Common bladderwort	0 1	3	
Vesiculina purpurea	Purple bladderwort		1	.

(Zizaniopsis miliacea), and by a tangle of shrubs, vines, and large herbs. The cut-grass not only is an ever present species in open cypress-gum swamps but forms a narrow zone along the borders of dense stands and is apparently a good site indicator for this community.

The marsh proper is well-developed, uniform and extensive. The predominant species are broadleaf cattail *(Typha latifolia)*, giant bulrush *(Scirpus californicus)*, and maiden cane *(Panicum hemitomon)* (Table 4).

TABLE 4. PRESENCE AND RELATIVE ABUNDANCE OF SPECIES IN FRESH WATER AND NEARLY FRESH MARSHES (TYPHA-SCIRPUS ASSOCIES AND MARISCUS CONSOCIES). *IMPORTANT SPECIES

SPECIES	Common Name	Raceland (0.0 percent salt)	Slidell (0.4 percent± salt)
Hibiscus lasiocarpus	Rose-mallow		1
Homalocenchrus oryzoides	Rice cut grass	3	
Jussiaea grandiflora	Primrose-willow	0 5	
**Mariscus jamaicensis*	Saw-grass		10
**Panicum hemitomon*	Maiden-cane	6	.
Phragmites communis	Roseau	2	
Pontederia cordata	Pickerel-weed	2	
Sagittaria lancifolia	Delta potato	1	4
**Scirpus californicus*	Giant bulrush	10	6
**Typha angustifolia*	Narrowleaf cattail	1	5
**Typha latifolia*	Broadleaf cattail	10	4
Zizaniopsis miliacea	Cut grass	2	1
AQUATICS			
Azolla caroliniana	Floating fern	0 5	
**Castalia odorata*	White water-lily	1	2
Ceratophyllum submersum	Coontail	3	
Lemna minor	Lesser duckweed	1	
Limnobium Spongia	Frog's-bit	0 5	
Myriophyllum proserpinacoides	Whorled water-milfoil	0 5	
Piaropus crassipes	Water hyacinth	2	
Riccia fluitans	Dissected liverwort	8	
Spirodela polyrhiza	Greater Duckweed	1	
Utricularia gibba	Humped bladderwort	1	
Utricularia macrorhiza	Common bladderwort	1	1

Of the three species the latter is somewhat less abundant here and may be scarce or absent in certain portions of the community. Cut-grass and roseau *(Phragmites communis)* occur as clumps throughout the associes but are of minor importance. Since the ground surface is usually covered with water (ave. 11.2 inches) there are several submerged and floating plants in the marsh proper. Of these species the coontail (*Ceratophyllum* sp.), duckweeds (*Lemna minor* and *Spirodela polyrhiza)* floating fern *(Azolla caroliniana)* and water hyacinth *(Piaropus crassipes)* are the most abundant (Table 4).

The open water of the fresh water habitat is often coated with duckweeds and the water fern and in some ponds with introduced water cabbage *(Pistia stratiotes)*. In many lagoons the deeper portions are occupied by a submerged community of coontail (*Ceratophyllum* spp.) and/or bladderwort (*Utricularia* spp.) whereas the shallower parts are invaded by cow-lily *(Nymphaea advena)* or white water-lily *(Castalia odorata)*. Among the most important aquatics is the beautiful, but pestilential, floating water hyacinth which sometimes packs an entire lagoon or chokes a bayou to a point where navigation is quite impossible. In certain areas the water milfoil *(Myriophyllum proserpinacoides)* joins with the water hyacinth in the free-floating community. A shore-attached creeping associes of the marsh button *(Achyranthes philoxeroides)* the primrose willow *(Jussiaea grandiflora)* is usually to be found along the shores of lagoons or bayous. In some cases these species completely overrun lagoons, ditches, and bayous with the con-

sequent destruction of all other aquatics, even including the vigorous water hyacinth.

The invasion of the marsh by the cypress-gum swamp is impeded by the occasional marsh fires which are decidedly unfavorable to the ecesis of trees. But the evidence points to a slow encroachment of the swamp trees into the marsh. The forest edge, composed mostly of willow and buttonbush, contains numbers of young bald cypress, water ash, and swamp maple trees. And there are many willow and buttonbush plants as well as young seedlings

FIG. 5. Fresh water transect showing oak forest, cypress-gum swamp, and fresh water mash (left to right).

of the above species in the marsh border. However, the average depth of the water in the forest border (11.7 inches) is greater than that of the marsh (11.2 inches). Since the first foot of marsh soil contains much more organic matter (30.6 percent) than that of the forest edge (18.2 percent) the greater depth of the water is probably due to a sinking of the soil level because of the decay of this organic matter. With this unexpected difference in water level explained the evidence all points to a succession towards the cypress-gum swamp.

SLIDELL TRANSECT

In the Slidell transect examples of loblolly pine forest (Pinus consocies), cypress-gum swamp (Taxodium-Nyssa associes), saw-grass marsh (Mariscus consocies), and a water-lily community (Castalia consocies) are all represented (Fig. 6). In addition there is a suggestion of the live oak *(Quercus virginiana)* forest on the lower edge of the pine forest as well as a poorly developed shrub zone on the marsh edge of the swamp forest. All these com-

FIG. 6. Slidell transect showing pine forest, cypress-gum swamp, saw-grass marsh (background, left to right) and water-lily lagoon (left foreground).

munities occur in the short distance of 40 feet, within which the decrease in elevation is about 17 inches—a sharp slope for South Louisiana. This transect is located in a nearly fresh (faintly brackish) area. Throughout the period of study only slight traces of salt were found in the surface water, but it seems probable that during violent storms which occasionally visit this region brackish water may invade the transect. The presence in the lower edge of the pine forest of salt up to 0.5 percent in the soil water is presumably due, at least in part, to such invasions.

The pine community is characterized by an even-aged, uniform, mature stand of loblolly pine *(Pinus taeda)* and considerable reproduction of loblolly pine and red gum *(Liquidambar styraciflua)*. On the front toward the marsh the soil level declines gradually to a point near the cypress-gum swamp where it dips rather steeply. Along the lower border of the pine forest couch grass *(Spartina patens)* and black rush *(Juncus Roemerianus)* are abundant, although they occur nowhere else in the area. These two plants are typically brackish marsh species, and their occurrence only in the edge of the pine lands might seem to be anomalous, since the average salinity of the soil water in the lower pine forest was 0.3 percent, as compared with 0.4 percent in the cypress zone. These figures, however, are probably misleading. The cypress zone was covered with water during the major portion of the year, so that soil water could be obtained only during three of the driest summer months. Data from the lower pine forest taken during comparable months show a salinity of 0.5 percent. It is probable, therefore, that the

soil water of the lower pine forest actually has a higher average salinity than that of the cypress swamp, so this factor may well account for the interesting distribution of these species.

The cypress-gum swamp fringes the pine forest in a belt about 15 feet wide. It includes only four trees of which bald cypress and swamp black gum *(Nyssa biflora)* account for at least 80 percent of the stand (Table 3). Although the average salinity of the soil water is only 0.4 percent tupelo gum, water hyacinth, and many other fresh water species are excluded. Several herbaceous species such as *Crinum americanum, Iris virginica, Myriophyllum pinnatum,* and *Proserpinaca pectinata,* were found in no other cypress-gum swamp studied. This is apparently due to the acid nature of the Coastal Plain soil upon which these communities are developed.

The nearly fresh (faintly brackish) marsh (Fig. 7) is characterized by a pure stand of saw-grass *(Mariscus jamaicensis)*. Associated with saw-

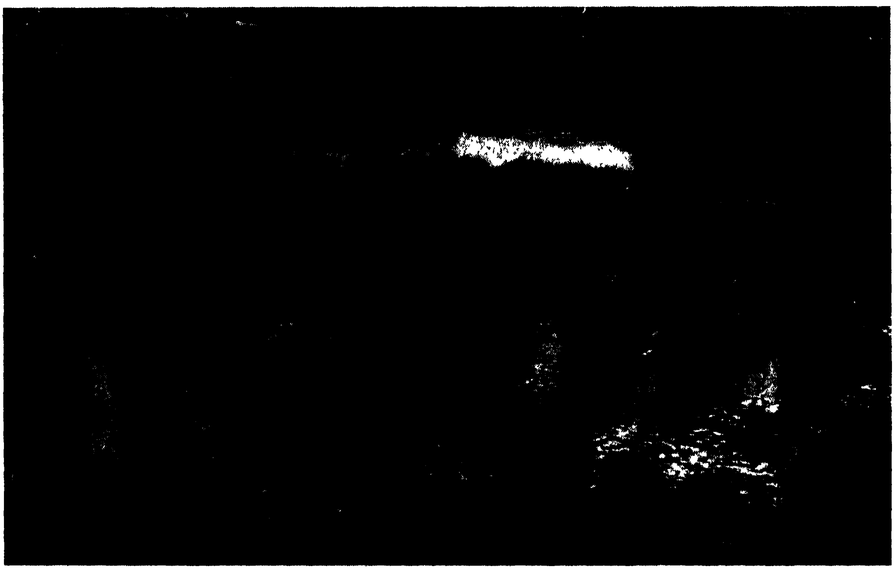

FIG. 7. Bird's-eye view of the saw-grass marsh (Mariscus consocies) showing numerous lagoons with water-lily pads.

grass, especially in deeper water, are broadleaf cattail, the narrowleaf cattail *(Typha angustifolia)*, and giant bulrush (Table 4). Since saw-grass is a large aggressive species it excludes most other plants and accounts for over 60 percent of the marsh vegetation. It is probable that saw-grass, water-lily, and bladderwort constitute over 95 percent of the total vegetation. Because of this dominance the marsh is noted for a striking paucity of species. Including the lagoons, in which the only aquatic species are the bladderwort and the white water-lily, there are less than 10 species in the marsh proper.

The succession in the lagoons of this area is initiated by a submerged stage of bladderwort *(Utricularia macrohiza)*, although white water-lily *(Castalia odorata)* is usually associated with it, especially in relatively shallow water. This is often followed by an early reed-marsh stage of narrow-leaf cattail and giant bulrush, which often fringe the water-lily lagoons,

TABLE 5. PRESENCE AND RELATIVE ABUNDANCE OF SPECIES IN THE SHRUB ZONES (BACCHARIS-IVA ASSOCIES). *IMPORTANT SPECIES

SPECIES	Common Name	Oak Island (0.5 percent salt)	Yellow House (1.4 percent salt)
SHRUBS AND VINES			
**Baccharis halimifolia*	Buckbrush	4	10
Convolvulus repens	Marsh bindweed	0.1	1
Cuscuta spp (on Iva)	Dodder	3	
Ilex vomitoria	Yaupon	0.5	
Ipomoea sagittata	Marsh morning-glory	2	2
**Iva frutescens*	Marsh elder	10	8
Rubus louisianicus	Swamp blackberry	1	
**Sabal minor*	Dwarf palmetto	4	
Sesban Emerus	Coffee bean	0.1	
Smilax Bona-Nox	Bristly greenbrier	0.5	
Vigna repens	Wild cowpea	1	
HERBS			
Aster exilis	Slim aster	1	
Bramia Monnieri	Hedge-hyssop	0.5	
Carex lupulina	Hop sedge		1
Eleocharis albida	White spike-rush	0.5	
Fimbristylis castanea	Sand rush	0.1	
Hydrocotyle verticillata	Marsh pennywort	0.1	
Iris giganticaerulea	Giant blue iris	2	
**Panicum virgatum*	Feather grass	1	2
Phragmites communis	Roseau	0.5	1
Ptilimnium capillaceum	Mock bishop-weed	2	
Rumex verticillatus	Swamp dock	2	
Sacciolepis striata	Gibbous panic-grass	0.5	
Solidago mexicana	Seaside goldenrod	3	
**Spartina patens*	Couch grass	10	4
Vicia ludoviciana	Louisiana vetch		1

although saw-grass may invade directly (Fig. 13). In the marsh saw-grass usually gains the upper hand but is shaded out along the swamp border and yields to the omnipresent cut-grass. It is evident that the cypress-gum swamp is invading the marsh only very slowly since the trees are scraggly and reproducing poorly. This is probably due in part to the salt in the soil water and also to the considerable depth of the marsh water (11.8 inches). The succession in this area apparently ends in loblolly pine forest, but there are numbers of red gum, live oak, and water oak *(Quercus nigra)* trees throughout the forest as well as numerous seedlings of the same trees. In other similar forests protected for longer periods from fire the broadleaved trees are gaining at the expense of the conifers. These facts lead us to believe that this forest is subclimax and that it would be replaced by the live oak forest if protected from fire over longer periods of time.

BAYOU VILLARS TRANSECT

The authors were especially interested in the transect at Bayou Villars since this was the only area where the cypress swamp bordered a distinctly brackish marsh. This transect is nearly one-half-mile long and extends across a low section of the oak forest (Quercus association), a considerable portion of cypress-gum swamp (Taxodium-Nyssa associes), a good sample of brackish marsh (Spartina-Distichlis-Juncus associes) and a cane zone (Phragmites-*Spartina cynosuroides* associes) on the low ridge along Bayou

TABLE 6. PRESENCE AND RELATIVE ABUNDANCE OF SPECIES IN THE CANE ZONE (PHRAGMITES-SPARTINA CYNOSUROIDES ASSOCIES). *IMPORTANT SPECIES

SPECIES	Common Name	Bayou Villars (0.5 percent salt)	Oak Island (0.9 percent salt)	Foster (1.2 percent salt)	Yellow House (1.6 percent salt)
Achyranthes philoxeroides	Marsh button	3		2	
Acnida cuspidata	Southern water-hemp			0.5	
Aster tenuifolius	Salt marsh aster			1	1
Baccharis halimifolia	Buckbrush	1		1	
Carex lupulina	Hop sedge	4		3	1
Chaetochloa magna	Giant foxtail			0.1	
Convolvulus repens	Marsh bindweed		3	2	2
Distichlis spicata	Salt grass		3		1
Hibiscus lasiocarpus	Rose-mallow	1			
Hydrocotyle verticillata	Marsh pennywort			0.5	
Ipomoea sagittata	Marsh morning-glory			2	0.5
Iva frutescens	Marsh elder			1	
Kosteletzkya virginica	Salt-marsh mallow		1	0.1	
Lythrum lineare	Marsh loosestrife			1	
**Panicum virgatum*	Feather grass		3	2	4
**Phragmites communis*	Roseau	10		3	
Rumex verticillatus	Swamp dock		1	1	
Sabbatia campanulata	Marsh pink		1		
Samolus floribundus	Brookweed			2	
Scirpus robustus	Three-cornered rush				1
Scirpus californicus	Giant bulrush	0.5			
Senecio glabellus	Butterweed	1		0.5	
Solidago mexicana	Seaside goldenrod	2	2		
**Spartina cynosuroides*	Quill cane		10	10	10
**Spartina patens*	Couch grass		4		4
Vigna repens	Wild cowpea		1		

Villars (Table 2). In the portion of the oak forest studied the level drops less than a foot to the cypress-gum swamp which is, in turn, about 6 inches higher than the marsh. As the bayou is approached the land rises again about 2 inches to the cane zone on the bayou bank. The water of Bayou Villars is usually almost fresh, the highest salinity noted being 0.1 percent, but the salinity of the soil water in the transect was distinctly higher. The lowest average soil salinity (0.3 percent) was found in the oak forest and about twice that amount was present in the cypress-gum swamp and cane zone. The highest salinity (1.1 percent), represented by a single determination in July, was in the marsh proper. Since soil water could be obtained here only during the dry weather of July, this figure is doubtless somewhat above the yearly average.

TABLE 7. PRESENCE AND RELATIVE ABUNDANCE OF SPECIES IN THE SALT GRASS COMMUNITY (DISTICHLIS CONSOCIES). *IMPORTANT SPECIES

SPECIES	Common Name	Foster (1.5 percent salt)	Yellow House (3.6 percent salt)	Popich (4.0 percent salt)
Aster tenuifolius	Salt-marsh aster	1		
Avicennia nitida seedlings	Honey mangrove			2
Baccharis halimifolia	Buckbrush	0.5		
Borrichia frutescens	Sea ox-eye		2	2
Chaetochloa geniculata	Marsh fox-tail	1		
**Distichlis spicata*	Salt grass	10	10	10
Fimbristylis castanea	Sand rush	3		
Iva frutescens	Marsh elder	1		
Juncus Roemerianus	Black rush	1	0.5	3
Panicum virgatum	Feather grass	1		
Pluchea camphorata	Spicy fleabane	2		
Scirpus robustus	Three-cornered rush	2	2	
Solidago mexicana	Seaside goldenrod	2		
Spartina alterniflora	Salt cane		2	2
Spartina cynosuroides	Quill cane	4		
Spartina patens	Couch grass	0.5	3	

The oak forest includes considerable numbers of live oak, water oak, red gum, and hackberry *(Celtis mississippiensis)*, although the body of the forest comprises live oak and red gum as the predominant trees. In the cypress-gum swamp the elevation very gradually decreases to the marsh. The upper portion of the swamp is characterized by considerable numbers of water ash, swamp maple, and black willow. These are all eliminated toward the middle of the swamp and the only tree companion of bald cypress in the lower half of the swamp is red bay *(Tamala pubescens)* (Table 3). Cypress is progressively more dwarfed and scraggly as the marsh is approached, especially in the relatively broad swamp-marsh ecotone. This is apparently due to the higher salinity of the soil water in the marshward portion of the swamp. Since the cypress-gum swamp is very open there is a considerable herbaceous population varying from typically fresh water species *(Echinodorus radicans, Persicaria punctata, Rynchospora corniculata,* and *Saururus cernuus)* in the upper portion of this swamp to brackish water species near the marsh border (Table 3).

Of all the marshes studied the one at Bayou Villars is at once the most most cosmopolitan and the most productive of species (Table 8). It possesses not only many species which are predominant in the fresh water marshes (for example, *Juncus effusus, Scirpus californicus,* and *Typha latifolia*) but also several which are exclusively found in brackish marshes (*Aster tenuifolius, Fimbristylis castanea, Scirpus Olneyi,* and *Spartina patens*) (Table 8). Of these species couch grass is by far the most frequent and abundant and probably constitutes over 50 percent of the total marsh vegetation. Furthermore it is in this transect that couch grass attains its greatest size. It should be noted that neither salt grass, nor black rush, which are the usual associates of couch grass, is to be found in this marsh.

As is true for other stands of this community the cane zone comprises very few species (Table 6). This is due to the large size and vitality of roseau, which constitutes at least 90 percent of the mass of vegetation. In more brackish areas quill cane *(Spartina cynosuroides)* is a codominant but is practically absent here.

TABLE 8. PRESENCE AND RELATIVE ABUNDANCE OF SPECIES IN THE BRACKISH MARSHES (SPARTINA-DISTICHLIS-JUNCUS ASSOCIES). *IMPORTANT SPECIES

SPECIES	Common Name	Bayou Villars (1.1 percent salt)	Oak Island (1.1 percent salt)	Foster (1.1 percent salt)
Achyranthes philoxeroides	Marsh button	2	.	
Acnida cuspidata	Southern water-hemp	1	1	0.5
Ammannia coccinea	Scarlet tooth-cup	0.1		
Ammannia Koehnei	Tooth-cup	0.1		
Aster exilis	Slim aster	1	0.5	
Aster subulatus	Salt-marsh aster		0.5	
Aster tenuifolius	Salt-marsh aster	1	0.5	1
Bramia Monnieri	Hedge-hyssop	2	0.5	
Chaetochloa geniculata	Marsh foxtail	0.1	0.5	1
Convolvulus repens	Marsh bindweed	0.5	0.1	
Cyperus Nuttallii	Nuttall's cyperus		0.5	
**Distichlis spicata*	Salt grass		6	6
Echinochloa Walteri	Wild duck millet	2	1	
Eleocharis albida	White spike-rush	1		1
Eleocharis microcarpa	Marsh spike-rush		1	
Eleocharis nodulosa	Marsh spike-rush	1		
Eleocharis parvula	Dwarf spike-rush			1
Eleocharis retroflexa	Dwarf spike-rush		1	
Fimbristylis castanea	Sand rush	3	2	1
Hibiscus lasiocarpus	Rose-mallow	1		
Hydrocotyle verticillata	Marsh pennywort	0.1		
Juncus effusus	Common rush	0.5		
**Juncus Roemerianus*	Black rush		3	6
Jussiaea decurrens	Primrose-willow	0.1		
Kosteletzkya virginica	False rose-mallow	0.1	0.5	1
Leptochloa fascicularis	Slender grass	1		
Lythrum lineare	Marsh loosestrife	2	2	1
Paspalum vaginatum	Joint grass	3	1	
Phragmites communis	Roseau	0.1		
Phyla nodiflora	Fog-fruit	2	0.5	.
Pluchea camphorata	Spicy fleabane			1
Rumex verticillatus	Swamp dock	1		0.1
Sabbatia campanulata	Marsh pink		0.5	.
Sagittaria lancifolia	Delta potato	2		...
Samolus floribundus	Brookweed	1		
Scirpus californicus	Giant bulrush	1	..	
Scirpus Olneyi	Bayonet rush	2	2	2
Scirpus robustus	Three-cornered rush		2	
Scirpus validus	Blue bulrush	1		
Sesban Emerus	Coffee bean	0.1	.	
Spartina alterniflora	Salt cane		1	1
**Spartina patens*	Couch grass	10	10	3
Typha angustifolia	Narrowleaf cattail	4	1	1
Typha latifolia	Broadleaf cattail	1	.	...
Verbesina alba	Verbesina	2	..	...
Vigna repens	Wild cowpea	1	...	....
AQUATICS				
**Ruppia maritima* (Lagoons)	Tassel-pondweed		..	10

TABLE 9. PRESENCE AND RELATIVE ABUNDANCE OF SPECIES IN THE SALINE MARSHES (SPARTINA ALTERNIFLORA CONSOCIES). *IMPORTANT SPECIES

SPECIES	Common Name	Yellow House (3.4 percent salt)	Popich (4 percent ± salt)
Distichlis spicata	Salt grass	2	2
**Juncus Roemerianus*	Black rush	10	1
**Spartina alterniflora*	Salt cane	10	10
Spartina patens	Couch grass	1	

TABLE 10. RELATIVE ABUNDANCE OF SPECIES IN THE HONEY MANGROVE COMMUNITY (AVICENNIA CONSOCIES). *IMPORTANT SPECIES

SPECIES	Common Name	Popich (4 5 percent salt)
**Avicennia nitida*	Honey mangrove	10
Batis maritima	Glasswort	2
Distichlis spicata	Salt grass	2
Spartina alterniflora	Salt cane	1

Apparently the cane zone is encroaching on the marsh, since young roseau occurs abundantly along the marsh border. Several facts seem to indicate, however, that the marsh grasses are invading the cypress swamp. In the first place, there is a virtual absence of seedlings and young trees of bald cypress except near the oak forest, whereas the older cypress trees are unhealthy in appearance. Moreover, "ghost forests" of dead cypress trees occur in the vicinity of the transect and many bald cypress stumps and logs largely or wholly covered by couch grass are found throughout the marsh near the swamp. Incursions of salt water from Barataria Bay which occur during heavy storms from the south undoubtedly kill and injure both seedlings and trees. In recent years these incursions have been facilitated by canalization in the area south of the transect, so it seems probable that the intervention of man has reversed the normal trend of succession and is enabling the marsh to push back the cypress swamp.

OAK ISLAND TRANSECT

Oak Island is a *chênière* situated in a brackish marsh and fringed by typical zonal communities. The transect, located on the northwestern rim of the *chênière*, includes portions of the live oak forest, the shrub belt (Baccharis-Iva associes), cane zone (Phragmites-*Spartina cynosuroides* associes), and the brackish marsh (Spartina-Distichlis-Juncus associes), but lacks the salt grass community (*Distichlis* consocies), which is present only on the southern forest border (Figs. 8, 9). This station presents more contour than most of the transects studied; the fall from the forest to the shrub zone is at least 14 inches, that from the shrub to the cane about 6 inches, and that from the cane to the marsh proper about 2 inches. On the south side of the ridge the land slopes very gradually to the marsh, but to the north it dips so steeply that all of the communities occur within the short distance of 30

feet. The lagoon at the lower end of this transect communicates indirectly with Lake Pontchartrain at times of high water, and has an average salinity of only 0.2 percent, showing almost no salt in late winter, but reaching 0.7 percent during the dry weather of midsummer. The soil water of the transect is, on the average, much more strongly brackish, the percentage of salt in-

FIG. 8. Brackish water transect showing oak forest, shrub, cane, salt grass, and brackish marsh communities (left to right).

FIG. 9. Oak Island transect showing brackish marsh (foreground), cane, shrub, and oak forest communities (left to right in background).

creasing steadily from the highest to the lowest communities (oak forest, 0.1 percent; shrub zone, 0.5 percent; cane zone, 0.9 percent; marsh proper, 1.1 percent).

The dominants of the live oak forest (Quercus association) are live oak and red gum, although several other tree species including six oaks are represented. This forest, the most prolific in species of all those studied, comprises nearly 30 shrubs and vines and over 60 herbaceous species. It is probable that the great number of species in this forest is due, at least in part, to human influence. On the southeastern margin the trees have been killed, probably by salt water, and the area is rapidly revegetating. Since the trees are too small and scattered to provide continuous shade the herbaceous population is almost wholly different from that of the forest proper.

The soil water here is too brackish for the growth of cypress and its associates but shrub and cane communities fringe the live oak forest in zones about 10 feet wide. In the shrub belt marsh elder *(Iva frutescens)* is most abundant although buckbrush *(Baccharis halimifolia)* and dwarf palmetto *(Sabal minor)* together about equal it in numbers (Table 5). Of the herbaceous components the versatile couch grass is predominant but marsh bindweed *(Convolvulus repens)*, marsh morning-glory *(Ipomoea sagittata)*, feather grass *(Panicum virgatum)* and seaside goldenrod *(Solidago mexicana)*, all characteristic of most shrub and cane communities, are well represented.

The cane zone occurs here where the average water table is near the soil surface (—0.9 inches). The important dominant is the agressive quill cane, although the smaller feather grass is abundant (Table 6). There is also a notable incursion of true marsh species, especially of couch grass and salt grass.

The brackish marsh is less cosmopolitan and much more uniform than that at Bayou Villars. This marsh, stretching away for miles with but little break in its greenish-brown cover, is among those labeled the "dreary marshes" by the writers of fiction. This uniformity is due to the fact that couch grass and salt grass, as the two major dominants, are similar in appearance and that the other principal species are not sufficiently different from these to lend much color or variety to the marsh physiognomy (Fig. 9). There are no large fresh water species here as at Bayou Villars but there are several new brackish and saline species in their stead. This marsh type is perhaps the most widespread of all and is important economically as the habitat *par excellence* of the Louisiana muskrat.

No submerged stages have been observed in the lagoons of this marsh area, although they are usually present in similar habitats elsewhere. Around the borders of lagoons the pioneer species are salt cane *(Spartina alterniflora)* and three-cornered rush *(Scirpus robustus)*. The pioneer species are followed by the dominants of the marsh proper which build up a thick substratum (1-3

feet deep) of peaty humus. The average amount of organic matter (based on the dry weight of the soil) is 55.0 percent in the first foot and 47.4 percent in the second foot of soil (Table 11). It might be assumed that the marsh in time would be succeeded by the cane belt and this successively by the shrub and forest communities as is suggested in Figure 14, but organic matter decomposes as it is elevated above the influence of salt water. The evidence, therefore, suggests that the succession here is conditioned primarily by the elevation of the marsh land by wind- and water-borne inorganic detritus and not by organic matter. In this process, of course, the plants play an important rôle in decreasing currents and otherwise contributing to the deposition of these sediments.

FOSTER TRANSECT

The most saline of the brackish stations is the Foster transect which is situated on Grand Bayou, a stream that is nearly fresh at its source but strongly saline near its mouth. Although the Foster area is somewhat more brackish than the one at Oak Island the zonal and marsh communities include the same species, although in different proportions. The transect, from the bayou front, extends across cane, salt grass, and marsh communities (Table 2). No shrub zone is included in the transect although some ex-

TABLE 11. AVERAGE EDAPHIC CONDITIONS IN MARSHES AND ADJACENT COMMUNITIES

	Water level[1] (*inches*)	Percent of salt in soil water[1]	Water content (percent of dry weight)[2]	Organic matter[2] Percent
RACELAND TRANSECT (Strictly fresh)				
Cypress-gum swamp	+ 7.8 (9)	0 0 (6)	139	16
			104	15
Forest border	+11 7 (9)	0 0 (4)	168	18
			142	11
Marsh	+11.2 (9)	0.0 (4)	207	31
			99	16
SLIDELL TRANSECT (Nearly fresh)				
Pine forest	−24 1 (9)	0.3 (8)	30	7
			27	5
Cypress-gum swamp	+ 2 5 (9)	0 4 (3)	77	21
			39	13
Marsh	+12 0 (6)		354	38
			254	29
BAYOU VILLARS TRANSECT (Slightly brackish)				
Oak forest	−23.6 (7)	0.3 (7)	33	6
			32	6
Cypress-gum swamp	− 5.4 (7)	0 6 (5)	68	16
			37	6
Marsh	+ 2.5 (6)	1.13 (1)	218	37
			109	17
Cane zone	− 4 1 (7)	0.5 (5)	167	23
			114	17

TABLE 11. (Continued).

	Water level[1] (*inches*)	Percent of salt water[1]	Water content (percent of dry weight)[2]	Organic matter[2] Percent
OAK ISLAND TRANSECT (Moderately brackish)				
Oak forest	—29 8 (11)	0 1 (9)	25	6
			28	5
Shrub zone	— 6 6 (12)	0 5 (11)	46	9
			35	8
Cane zone	+ 0 7 (12)	0 9 (6)	195	29
			135	29
Marsh	+ 2 1 (12)	1 1 (5)	475	55
			452	47
FOSTER TRANSECT (Strongly brackish)				
Cane zone	— 4 7 (9)	1 2 (9)	178	25
			154	19
Salt grass	— 1 0 (9)	1 5 (6)	592	46
			316	18
Marsh	— 0 6 (9)	1 1 (6)	729	57
			389	45
YELLOW HOUSE TRANSECT (Saline)				
Shrub zone	— 9 8 (10)	1 4 (10)	57	10
			82	8
Cane zone	— 5 4 (10)	1 6 (10)	113	13
			111	8
Salt grass	— 0 4 (10)	3 7 (8)	154	17
			148	17
Marsh	+ 0 7 (10)	3 4 (3)	259	24
			273	23
POPICH TRANSECT (Strongly saline)				
Honey mangrove	- 2.2 (10)	4 5 (9)	106	9
			118	11
Salt grass zone	+ 1 3 (10)	4 0 (3)	110	10
			150	11
Marsh	+ 2 3 (10)	not determined	142	10
			163	14

[1] Under "Water level" the + and — signs indicate levels above and below the soil surface The number of determinations of water level and salinity on which each of the averages is based is indicated in parenthesis

[2] Under "Water content" and "Organic matter" the two figures given refer to the first and second feet of soil, respectively. Each of these figures is an average of 2 to 4 determinations

amples occur in the region. The difference in ground level between the highest and lowest parts of the transect is only about 4.5 inches, since the cane zone averages 3 inches higher than the salt grass zone which, in turn, is about 1.5 inches higher than the marsh proper. As regards salinity of soil water, the three plant communities are remarkably similar, the average salinity in the cane zone being 1.2 percent; in the salt grass zone, 1.5 percent; in the marsh, 1.4 percent.

In the cane zone (Phragmites-*Spartina cynosuroides* associes) quill cane is the major dominant although roseau and feather grass are represented as minor codominants (Table 6). The cane community here is similar to that in the Oak Island transect except that it embraces a greater number of

species. Since the average water table is lower here (—4.7 inches) than at Oak Island, where it is very close to the soil surface, the cane zone includes fewer marsh species and none of the true marsh dominants.

The salt grass belt (Distichlis consocies) is a distinctive community characterized by the relatively small and attractive salt grass. This species forms practically a continuous stand, although scattered plants of many species appear throughout the community. The sea ox-eye *(Borrichia frutescens)* which is the most common associate of the salt grass elsewhere, is not found here (Table 7).

The brackish marsh (Spartina-Distichlis-Juncus associes) in the Foster transect is of more than passing interest since it represents the last stand of the couch grass under increasingly saline conditions (Fig. 10). Of the dom-

FIG. 10. Brackish marsh (Spartina-Distichlis-Juncus associes) at the Foster transect.

inants salt grass and black rush are about equal in numbers but couch grass is much less abundant (Table 8). Of the other components bayonet rush *(Scirpus Olneyi)* and the spike rushes *(Eleocharis albida* and *E. parvula)* are numerous near muskrat houses, probably due to the creation of relatively bare areas by muskrat activity. In addition four species, common to higher communities, were found growing on abandoned, decomposing muskrat mounds. In this marsh the organic content of the soil was higher than in any other. This has led to the conclusion that peaty humus accumulates most rapidly where the salinity is low enough to permit excellent plant development and yet sufficiently high to prevent rapid decay. These conditions obtain in the marsh of the Foster area.

The lagoons become choked with the tassel pondweed *(Ruppia maritima)* into which the marsh dominants soon enter (Fig. 13). However, ditches are invaded by salt cane which usually forms a pure stand. These habitats are not readily entered by the marsh dominants since considerable elevation must be accomplished before they can survive. It is probable that the salt grass zone is encroaching on the marsh since there is vigorous reproduction of salt grass in the border zone, but there is little evidence that the cane zone is infringing on the salt grass community.

YELLOW HOUSE TRANSECT

The topography along the bayou front here is very different from that in any other transect. It is the practice of fishermen to dump old oyster shells in the shallow water along the shore of the bayou. Here a ridge of partially decomposed shells is covered by about 10 inches of clayey mud which also fills the interstices between the shells. In addition a fore-land of fine sediments about 8 feet wide and about 3 inches lower than the ridge has been laid down on the bayou side. The transect, from the bayou edge, extends across a salt grass community, a shrub zone on the crest of the ridge and, at successively lower elevations, cane, salt grass, and true marsh communities. Since the two salt grass zones are similar except for a greater abundance of sea ox-eye in the bayou front community, only the innermost is listed in Table 7. From the highest to the lowest community the average ground level falls about 9 inches in 100 yards, the slope from shrub zone to cane being 4 inches, from cane to salt grass, 4 inches, from salt grass to marsh, 1 inch. Striking variations in salinity of soil water are noted at the different levels, as indicated by the yearly averages in the four communities: shrub zone, 1.4 percent; cane zone, 1.6 percent; salt grass zone, 3.6 percent; marsh, 3.5 percent.

The shrub belt (Baccharis-Iva associes), because of its comparatively low salinity, supports several species that are relatively intolerant of salt, among which are buckbrush and roseau. Of the dominants buckbrush is more abundant than marsh elder. As is usual in shrub zones marsh bindweed, marsh morning-glory and couch grass are present, the latter in considerable abundance. It will be noted, however, that the number of species represented is much lower than that in the Oak Island transect (Table 5).

The cane community (Phragmites-*Spartina cynosuroides* associes) is similar to the one at Foster but includes less than half as many species. Of the dominants quill cane, considerably outnumbers both roseau and feather grass. The salt grass zone (Distichlis consocies) comprises only five species, two of which, black rush and salt cane, are dominants of the marsh proper. Of the other three species, sea ox-eye and couch grass are common but salt grass constitutes over half of the total vegetation in the community (Table 7). It is of interest that couch grass, the main dominant of brackish marshes,

is here more abundant in every zonal community than it is in the marsh proper.

Couch grass and salt grass which are major dominants of brackish marshes, are very rare in the saline marsh (*Spartina alterniflora* consocies). The major dominant in the saline marsh is usually salt cane, but black rush is an important codominant in this area. This is a marsh with high salinity, moderate organic matter (24.3 percent) and a paucity of both plant and animal species. Nevertheless this marsh is of great importance in reclaiming shallow lagoons and mud banks throughout the saline areas bordering the Gulf, the successional stages being very similar to those in the Foster area.

POPICH TRANSECT

The Popich transect is unique in that it includes a total of only six plant species, among them the remarkable honey mangrove *(Avicennia nitida)*. The transect cuts across a wide zone of honey mangrove, a band of salt cane, a narrow belt of salt grass and ends in the low salt cane marsh (Fig. 11). This zonation differs from the typical pattern of the area in the presence of the band of salt cane next to the mangrove. It is difficult to account for this band of salt cane since its elevation is even greater than that of the salt grass community. In any case the salt grass zone is usually adjacent to the honey mangrove whereas the salt cane is usually found at lower elevations.

The crest of the bayou "ridge," occupied by the mangrove zone, stands 3 inches above the main body of the marsh, and was never seen under

FIG. 11. Saline transect showing honey mangrove, salt grass, and saline marsh communities (left to right).

water except at times of strong onshore winds. In the outer salt cane belt (2 inches lower than the mangrove) the water level is typically just above or just below the soil surface, and the same is true of the salt grass zone which is one-half-inch still lower. A further drop of about an inch marks the transition to the marsh proper, which was never seen without standing water. Salinity in the bayou (varying with season and weather from 0.9 to 3.2 percent) averaged 2.3 percent, and in the surface water of the marsh it

FIG. 12. Popich transect showing honey mangrove and marsh communities (left to right).

averaged nearly the same. The soil waters, however, were more strongly saline (mangrove zone, 4.5 percent; outer salt cane zone 3.7 percent; salt grass zone, 4.0 percent). No soil water determinations were obtained from the marsh proper because of the continual presence of surface water.

Without doubt the honey mangrove zone (Avicennia consocies) is the most striking of all the marsh communities (Fig. 12). It is characterized by a dense stand of honey mangrove with a scattering of glasswort *(Batis maritima)* (Table 10). Honey mangrove is an evergreen shrub, up to 25 feet in height, characterized especially by terete, aerenchymous root knees about 16 inches high. These knees are probably of value in gaseous exchange although the average water table is 3 inches below the soil surface. Since honey mangrove readily invades the lower communities and would occupy a much larger area except for annual marsh fires, the "knees" are probably of real service in ecesis in the wetter habitats. In addition the soil is covered by storm tides several times in the course of a year. The fruit of honey mangrove, including one seed with two peculiarly folded cotyledons is shed in

December. When the soil surface is covered with water in the winter and early spring these fruits germinate as they float about over the various marsh communities. When the water recedes the hairy radicles take root and seedlings develop. Since the salinity of the surface water is usually less than 1 percent in the winter whereas that of the soil is around 4 percent this method is considered as a means of survival since the seeds are said not to germinate readily in a medium of high salinity (Joshi, 1933).

The salt grass zone (Distichlis consocies) closely resembles the stands of this community found elsewhere. Salt grass forms an almost continuous stand in which occur scattered plants of its common associate, sea ox-eye (*Borrichia frutescens*). The only other species found here are black rush, salt cane, and seedlings of honey mangrove (Table 7). These mangrove seedlings occur mainly in the upper edge of the zone, whereas salt cane is somewhat more abundant in the lower portions; otherwise the species named are about equally frequent throughout the community.

The saline marsh (*Spartina alterniflora* consocies) presents a nearly pure stand of the salt cane (Table 9). The plants of this species are notably dwarfed, and they blend, in general appearance, with the much less abundant salt grass, so that only the occasional patches of black rush serve to break the monotony of the great stretches of this dreary marsh. The upper two feet of soil in this marsh are well filled with rhizomes and roots, providing a fairly solid substratum; but, though some roots continue to a depth of 5 feet, the soil is so mucky and fluid that a 3-inch auger may easily be pushed from the 18-inch to the 5-foot level with one finger. The organic content of the soil is relatively low (10.3 percent for the first foot of soil and 14.4 percent for the second foot). Presumably this is due to the fact that the plant structures decompose very slowly while silt is being deposited rather rapidly, every storm from the South submerging the area in water and depositing a film of sediment. The importance of salt cane in stabilizing these deposits is obvious.

The deeper lagoons of this marsh are usually free of plants, except for a few algae, but salt cane readily invades the shallower portions, and as the marsh is being built up, the higher communities are definitely advancing over the lower (Fig. 13). This is particularly evident in the case of honey mangrove. Not only is there a gradation in size of mangrove away from the bayou, but there is abundant migration of its seedlings into the grass communities. Furthermore, there is a considerable mass of partially decomposed rhizomes and roots of marsh species even under the densest stand of honey mangrove.

GENERAL NOTES ON VEGETATION

In the preceding descriptions the areas studied have been classified, on the basis of salinity, into two major habitat groups, the *fresh water* and the *salt water* habitats. The fresh water habitats include not only the *strictly fresh*

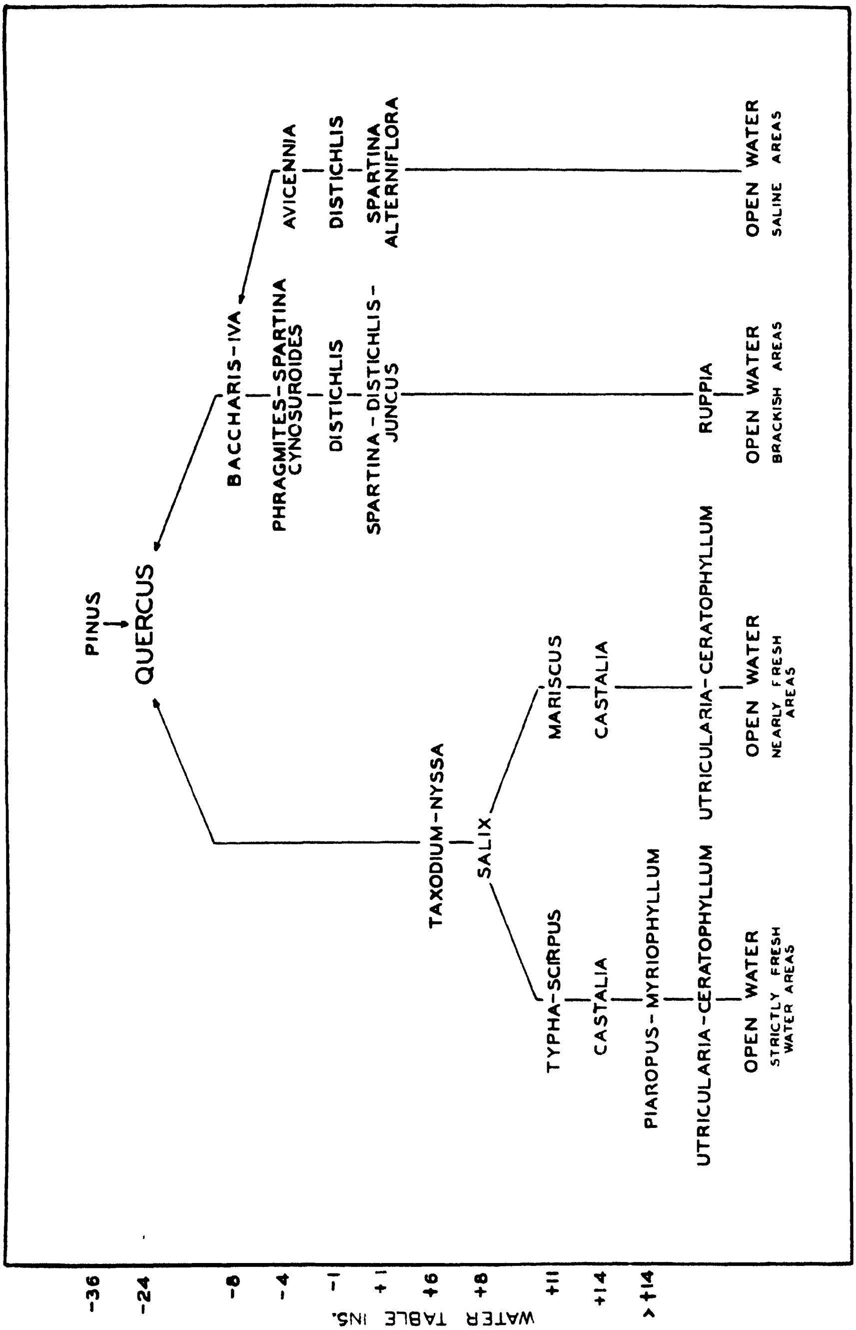

FIG. 13. Chart showing the probable successional relations of the plant communities of the marsh habitats.

water areas, but also the *nearly fresh* (faintly brackish) areas, in which the average salinity of the soil water does not exceed 0.5 percent. The *brackish* areas which have salinities of 0.5 to 2.0 percent and the *saline* areas in which the average salinity range is from 2.0 to 5.0 percent have been included as salt water habitats. The reasons for making the diversion at this point will become apparent later.

In the fresh water habitats the elevations in the marshes, if high enough, support pine or oak forest which is replaced, at lower levels, by cypress-gum swamp and marsh. As observed by the writers the pattern is always the same —pine or oak forest, cypress-gum swamp, marsh. The outstanding feature of these marshes is the presence of sedges or grasses 8 to 12 feet tall. Two distinct marsh associes are recognized in these areas. The *strictly fresh water* marsh is populated by broadleaf cattail and giant bulrush, whereas the *nearly fresh* (faintly brackish) marsh is given over largely to saw grass. In addition the nearly fresh water areas include several species typical of salt water marshes but only in the lower zonal communities where there is an appreciable amount of salt in the soil water.

In salt water habitats the vegetation pattern is quite different. Cypress-gum swamp is absent, and pine or oak forest is flanked, at successively lower levels, by zones of shrub, cane, and salt grass, beyond which lies the marsh whose dominant species, low in stature (2 to 4 feet), are in striking contrast with the towering species of the fresh water marshes. Since the shrub, cane, and salt grass communities form belts around the forest they are referred to as *zonal communities*. Our evidence seems to indicate that the transition from 0.4 percent to 0.6 percent in the average salinity of the soil water is responsible for the elimination of the cypress-gum swamp and the appearance of the zonal communities.

The zonal communities of shrub, cane, and salt grass present several points of interest. Like the cypress-gum swamp of the fresh water areas, they stand between the oak forest and the marsh, but whereas the cypress is typically found in permanent standing water, these zonal communities are usually present where the average water level is one or more inches below the surface. Among these communities the shrub belt stands out in bold relief because of the size and evergreen character of the dominant species. The cane zone, although occurring at a slightly lower elevation than the shrub belt, is also conspicuous, since it occupies a much greater area than the shrub community and is composed of very large grasses from 8 to 16 feet high. The salt grass belt is not conspicuous because of the small size of the predominant species. Near the coast it is often partially or wholly replaced by a conspicuous evergreen community of honey mangrove. The zonal communities usually fringe the rivers and bayous; hence the traveler in the marshlands, whether going by boat or by highways built on the bayou banks, is apt to gain the impression that these communities are very impor-

tant components of the marshland vegetation. However, from various survey trips we have estimated that they occupy less than 5 percent of the total marshland area.

The shrub zone is poorly developed in fresh water areas, but it is usually well developed in brackish habitats wherever the soil level is high enough. On the other hand the cane zone or salt grass or both may be entirely absent. The cane zone is usually absent in the most saline habitats (Popich transect, Grand Isle, Louisiana, and Cat Island, Mississippi) whereas salt grass is lacking in slightly brackish habitats (Bayou Villars and Oak Island transects). Of the dominants in the cane zone roseau is rare in highly brackish habitats and even quill cane is eliminated in the saline habitats in the immediate vicinity of the Gulf. Instead the salt grass zone is bordered at higher elevations by a shrub zone in which marsh elder and sea ox-eye are the important shrubby components.

In salt water habitats the low ground of the paludal basins is occupied by a typically extensive marsh in which water from one to a few inches deep typically stands on the surface through most of the year. The writers have recognized two marsh communities in the salt water area—the brackish marsh (Spartina-Distichlis-Juncus associes) and the saline marsh (*Spartina alterniflora* consocies). The brackish marsh may be represented by pure stands of couch grass in slightly brackish areas or by pure stands of black rush in sandy areas but there is usually an admixture of one or both of these species with salt grass. Of the three dominants couch grass is the least tolerant of salt and, therefore, is replaced by the other two in strongly saline areas. Since both black rush and salt grass have wide ranges of salt tolerance which overlap with that of salt cane, the dominant of the saline marsh, the brackish marsh merges insensibly into the saline marsh. These facts emphasize the difficulty of delineating these marsh communities and indicate that the present nomenclature must be regarded as tentative.

Several cases of peculiar distribution of species should be mentioned here. Cut-grass is most abundant on the marshward fringes of the cypress-gum swamp-forest and is usually a good site indicator for this forest. In addition it is very abundant in young marshy areas which young cypress trees are invading. It may even occur in nearly pure stands over a considerable area in which case it approximates a true marsh community, but it is never of importance in well developed marshes. It appears, therefore, that it often forms a marsh-like seral stage but is replaced later either by mature marsh or the cypress-gum swamp. The two tall "canes", *Phragmites communis* and *Spartina cynosuroides*, typically occur in a cane zone where the average water level was found 3.4 inches below the soil surface. However, in relatively fresh water areas they occur where the average water level is near or even above the soil surface and may even approximate the status of true marsh dominants. This is true in many localities near Lakes Borgne and

Pontchartrain and near the mouth of the Mississippi River. *Distichlis spicata* is a versatile species which not only occurs in nearly pure stands in the salt grass zone throughout the salt water habitats but it is a very wide-ranging marsh dominant from slightly brackish to very saline conditions. *Juncus Roemerianus* is an important marsh dominant in the brackish and saline marshes but attains its maximum abundance and size in sandy areas where it constitutes what Mohr calls the "black rush formation."

The successional relations in the marsh habitats are not known with certainty, but from the juxtaposition of communities, and especially from their relations to the average water levels, some idea of the probable course of succession may be deduced (Fig. 13). Doubtless there is considerable deviation from this typical pattern, especially in regard to the successions leading to the marsh, shown in the two lines at the left in Figure 13. Furthermore it should be noted that no attempt has been made to suggest what the secondary successions might be. Investigations are now under way to determine these detailed successional relationships.

EDAPHIC FACTORS

Of the factors governing the composition and distribution of marsh communities it was clearly evident from the beginning that the edaphic factors were of first importance. After preliminary tests we decided to make routine determinations of the following factors in every community: (1) the water level with reference to the soil surface; (2) salinity of free soil water (or of surface water when present) and that of adjacent bayous and lagoons; (3) water content of the soil, based on dry weight; and (4) percentage of organic matter in the soil. Organic matter was tested from two to four times at each station; all other determinations were made, so far as practicable, once a month for 12 months. It was clearly recognized that certain other determinations, such as pH, dissolved oxygen, and salinity of capillary water, would have been highly desirable, but time limitations made it impossible to include them.

It is perfectly obvious that tests made once a month throughout one year do not constitute a quantitatively accurate study of fluctuating factors such as water level and salinity, but we feel that the data thus obtained do make possible a significant comparison of living conditions at the different stations. The comparisons between the communities of a given transect are believed to be fairly satisfactory since, in each case, all the zones were studied on the same day and under approximately the same conditions. The comparisons of the different transects are not quite so satisfactory because of variations in weather conditions under which the different stations were visited. Our records show, however, that a wide range of wet and dry conditions, in both winter and summer, was encountered at each transect.

SALINITY

METHODS

The study of salinity has been based mainly on free soil water. Surface water was tested also, but, except as it influences soil water, it is not believed to be of great importance in determining the distribution of plant communities, since the absorbing organs of plants are rarely in contact with surface water. Therefore, unless otherwise stated, the *salinity data for each community refer to the salinity of its free soil water.*

The method of taking samples was as follows. On each of the monthly trips to a given area surface water was collected from the transect, if present, and also from the adjacent bayou or lagoon. Soil water was collected, so far as possible, from each community by boring a hole of appropriate depth with a soil auger and allowing it to fill to approximately constant level from the surrounding soil. It will be noted (Table 11) that there is great varation in the number of soil water samples obtained in the different zones of a transect. This is due to the frequent presence of surface water in the lower communities and to the depth of the water table in the higher communities. For example, in the marsh proper at the Raceland, Slidell, and Popich transects, no soil water samples were obtained, due to the continual

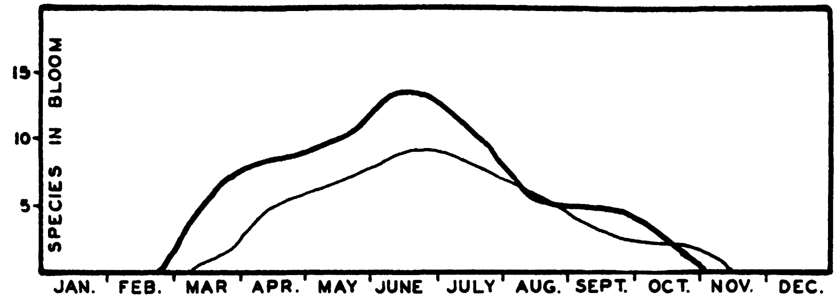

FIG. 14. Relative anthesis in the strictly fresh water marsh at Raceland and nearly fresh water marsh at Slidell (light line).

presence of surface water, and in several other communities the same condition obtained except in dry weather. On the other hand, in the forests at the Slidell and Oak Island transects, the water table could be reached with a 6-foot auger only after heavy rains.

Salinity determinations were made hydrometrically by a method which was standardized during the early stages of the work. Several of the determinations were checked by gravimetric and volumetric methods which seemed to indicate that the hydrometric determinations were accurate to within 0.1 percent of salt. A fuller discussion of the method used and factors influencing the results will be presented in a separate paper.

RESULTS

In the presentation of our findings we have dealt mainly with averages rather than with individual determinations, since the salinity at a given point fluctuates widely with season and weather. Therefore, unless otherwise indicated *each datum on salinity of either soil water or surface water is the average of the determinations made on all the monthly samples collected at a given point.* The evidence now in hand, the most important parts of which are summarized in Table 11, seems to justify the following conclusions:

1. *The salinity of surface water in the marshes does not greatly exceed that of the adjacent lagoons, bayous, and lakes.* Presumably this is due partly to the heavy rainfall and partly to the innumerable lagoons in which, at most points, frequent interchange occurs between tidal pools and the permanent open waters. At the Oak Island transect, where the surface water of the marsh and that of the lagoon are continuous after every

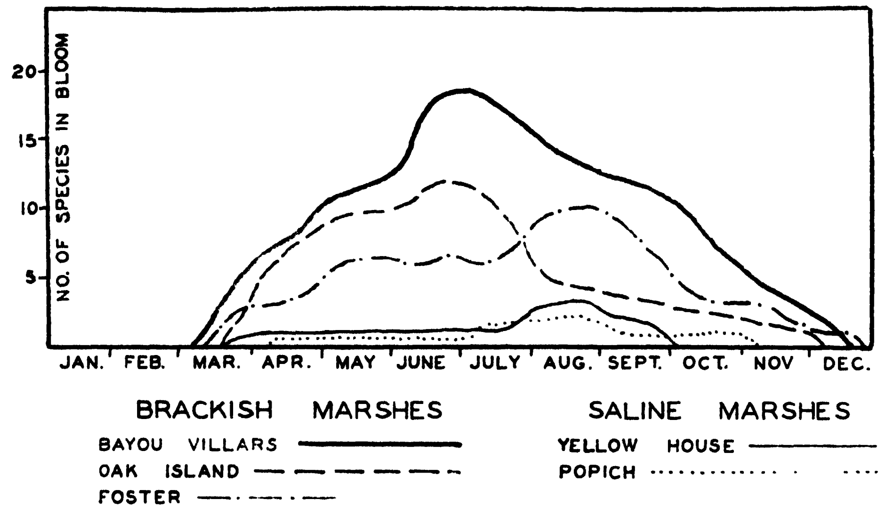

FIG. 15. Relative anthesis in the brackish and saline marshes.

heavy rain, the average salinity in both is identical (0.2 percent), but at the Yellow House transect where a bank several inches high prevents communication between bayou and marsh except at times of very high water, the salinity in the surface water of the marsh averages 2.4 percent as compared with 2.0 percent in the bayou.

2. *The free soil water in marsh communities, as a rule, is decidedly more saline than the water of nearby lagoons, bayous, and lakes.* At the Popich transect, for example, the water of Grand Bayou contained, on the average, 2.3 percent of salt while the soil water of the honey mangrove zone showed nearly twice that concentration (4.5 percent). In the nearly fresh (Slidell) transect the proportionate difference is even greater, the 0.4 percent of salt

in the soil water of the cypress-gum community being at least eight times the average amount present in the permanent standing water of the marsh. In only three of the twenty-four communities listed in Table 11 (forest at Oak Island, shrub and cane zones at Yellow House) was the soil water found to be less saline than the adjoining body of open water, and all these communities were situated 5 inches or more above the average level of the open water. Just how the relatively high salt concentrations in the soil are maintained in the presence of a 60-inch rainfall is a question of considerable interest. Obviously surface evaporation and transpiration play a part, but their relative importance is by no means clear.

3. *The highest salinity in an area is usually found in a community where the average water level is just above or just below the soil surface.* This is not surprising, since surface evaporation from saturated soils should be rapid, and leaching should be expected to be relatively ineffective at these low levels. The following comparison illustrates the principle.

Transect	*Community of highest salinity*		*Average water level in that community*
Popich	Honey mangrove	(4.5 percent)	-2.0 inches
Yellow House	Salt grass	(3.7 percent)	—0.4 inch
Foster	Salt grass	(1.5 percent)	—1.0 inch
Oak Island	Marsh proper	(1.1 percent)	+2.0 inches
Slidell	Cypress gum .	(0.4 percent)	+2.5 inches

These data bring out the additional fact that, in the transition from saline to nearly fresh water areas, the zone of greatest salinity was found at progressively lower elevations. The significance of this fact is by no means clear.

4. *With progressive elevation of the soil surface more than a few inches above the water level of the bayou or lagoons there is a progressive decrease in the salinity of the soil water.* At the Yellow House transect, for example, where the marsh proper is just about at the level of the water in Grand Bayou, the salt grass zone with its high salinity of 3.7 percent is approximately 1 inch above the marsh; 4 inches higher in the cane zone the salinity drops to 1.6 percent, and another rise of 4 inches brings us into the

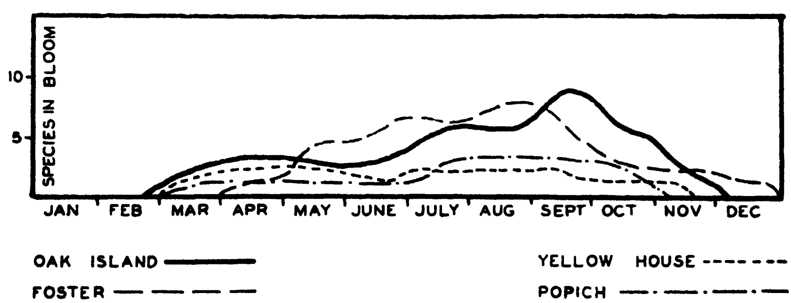

FIG. 16. Relative anthesis in the salt grass communities.

shrub zone on the crest of the bayou ridge where the salinity is only 1.4 percent. These decreases are especially noteworthy in view of the large size and high evaporating power of the shrub and cane communities whose plants, 8 and 10 feet tall, are in striking contrast with the scarcely knee-high salt grass.

5. *The marsh types in Southeastern Louisiana are closely correlated with salinity.* The stricty fresh-water marsh (Typha-Scirpus associes) is found in areas where the hydrometer shows no trace of salt. The saw grass marsh (Mariscus consocies) occurs where the salinity is less than 0.5 percent. Although no soil water samples were obtained in the saw grass marsh at the Slidell transect this conclusion is supported by the determinations made in the other communities at that transect and also by data obtained from other stands of the saw grass community. The average salinity of the brackish marsh (Spartina-Distichilis-Juncus associes) varies from 0.5 to 2.0 percent, and that of the saline marsh (*Spartina alterniflora* consocies) ranges from 2.0 to 5.0 percent (Fig. 17). Since every plant has its own range of salt tolerance there is a gradual transition from the nearly fresh to the saline marsh type, with broad ecotones, often several square miles in extent, connecting them.

WATER LEVEL

Anyone who wades the marshes of South Louisiana may readily observe that the water in salt water marshes is not as deep as it is in fresh water marshes. In saline areas the vegetation does not usually invade deep water, a depth of 4 inches or more being found only in open lagoons, whereas, in fresh water areas, a tall marsh vegetation commonly stands in water a foot or more deep. More careful study shows that, in the transition from brackish to fresh water conditions, both zonal and marsh communities are found growing at progressively lower elevations. Four examples of this principle may be cited. Quill cane dominates the cane zone in 3 of the transects studied. At Yellow House (salinity 1.6 percent) it is 5.4 inches above the water table; at Foster (1.2 percent salt) it is 4.7 inches above water table; but at Oak Island (0.9 percent salt) water averaging nearly an inch in depth covers the cane zone. The same general relations are shown by the shrub zone, the cypress-gum swamp, and the brackish marsh (Table 11).

All these observations are closely related to certain facts discussed in the section on salinity. For example, in the saline Yellow House area, the shrub and cane communities have established themselves only on the higher ground where salinity is much less than in the marsh proper, but at stations farther inland, where the zone of greatest salinity occurs at lower levels, the shrub and cane communities are found thriving at progressively lower elevations.

The relations of salt grass to water level are quite different from those just described, for, in going from saline toward fresh water habitats, it is found at progressively *greater* elevations. At the Popich transect (4.0 per-

cent salt) it is covered by more than an inch of water; at Yellow House (3.7 percent salt) it is nearly half an inch above the water table; and at Foster (salinity 1.5 percent) it is 1 inch above average water level.

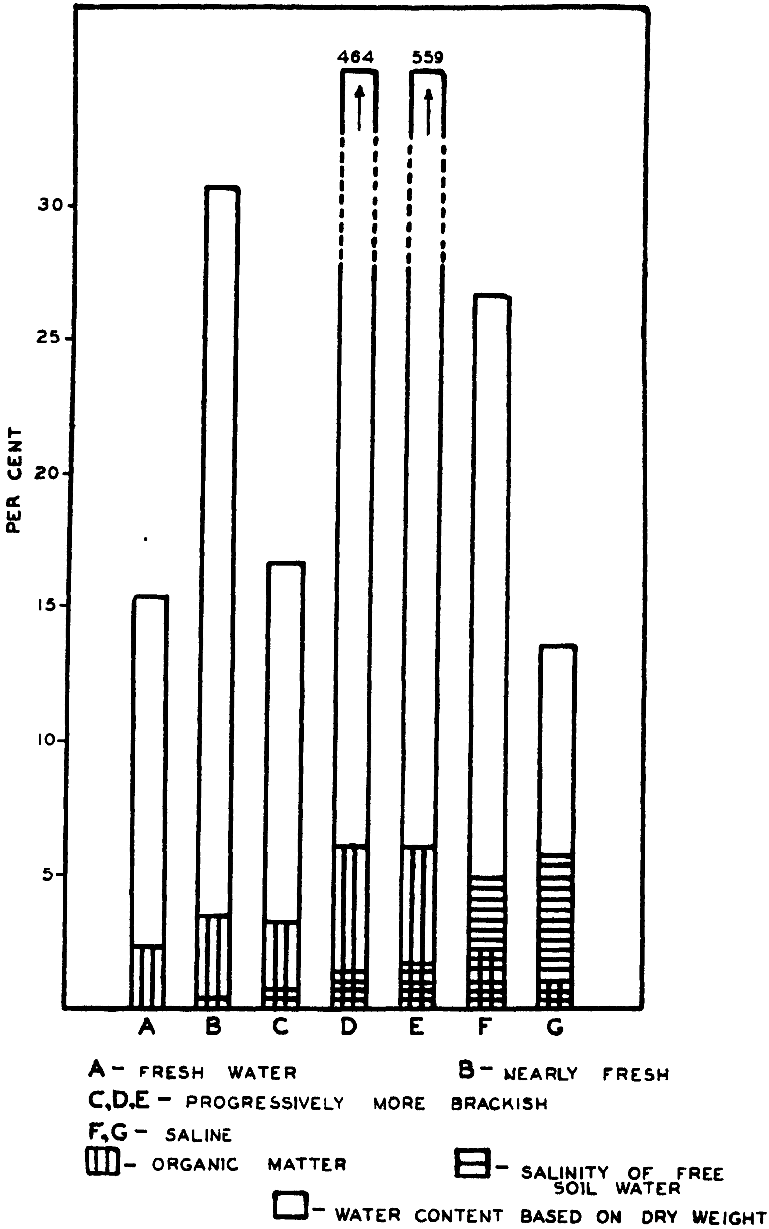

FIG. 17. Average edaphic conditions in the true marshes.

The reason for this reversal of relationships is not fully understood, but apparently salt grass, unlike the typical brackish water species, is favored by high salinity and normally occupies the most saline parts of every area where it grows unless crowded out by honey mangrove. In relatively fresh water areas the greater number of communities occurs where there is considerable surface water but in brackish or saline areas nearly all the communities occur where the mean water table approximates or is somewhat below the soil surface (Fig. 13). In fresh water ponds submerged, free-floating and attached floating communities are usually present but the only aquatic stage present in brackish lagoons is a submerged community and even this is absent in saline water bodies. Since the cypress-gum swamp borders directly on the marshes of fresh water areas, the shrub and cane communities, so typical of brackish areas, are absent in these habitats.

WATER CONTENT AND ORGANIC MATTER

In marsh communities the average percentage of soil water, as based on the dry weight of the soil, ranges to an astounding degree. During the period of investigation the least soil water (8.1 percent) was found in the first foot of soil of the oak forest at the Oak Island transect on July 24, 1932, and the greatest amount of water (867.1 percent) was obtained exactly one month later in the first foot of soil in the brackish marsh in the Foster transect. The average water contents of the pine and oak forests (25 to 32 percent) are not unlike those reported elsewhere, but the average in soils of marsh communities (98 to 728 percent) are striking and rarely encountered in ecological literature (Table 11). From the above figures it is evident that the water is from 0.98 to 7.28 times the weight of the solid material which constitutes the soils. In general the percentage of soil water was lowest on the *chênières* and ridges and greatest in the marsh proper. The percentage of water was thus progressively higher in the following communities: pine forest, oak forest, shrub zone, cypress-gum swamp, cane belt, salt grass zone, and marshes (Table 11).

In general, the organic content (based on dry weight) is least on the islands and ridges and progressively greater at lower elevations. The lowest percentage of organic matter (3.0 percent) was found in the first foot of soil in the pine forest of the Slidell transect and the greatest amount (59 percent) in the first foot of soil of the marsh of the Foster transect. In the marshes proper, it is relatively low in both fresh water and saline areas and progressively higher toward the brackish marshes (Fig. 17). The same sequence is true for the water content of marsh soils. Thus the average water content in the first two feet of soil is relatively low (153 percent) in the fresh water marsh, becomes progressively higher in the more brackish areas until it reaches a peak in the highly brackish marsh (559 percent) and relatively low again (142 percent) in the saline marshes (Fig. 17). The rel-

atively high water content of brackish marsh soils is undoubtedly due to the high percentage of organic matter contained therein. This in turn, is probably due to the favorable balance of plant growth over plant decomposition. In fresh water marshes growth and decomposition are rapid; in saline marshes both processes are slow; but in brackish marshes growth is excellent whereas decomposition is greatly retarded.

In soils which are rarely saturated the ratio of water content to organic matter is relatively low and fluctuating but in the soils of lower communities this ratio is high (about 10 to 1) and comparatively constant. Stated otherwise, the amount of organic matter in saturated soils is approximately 10 percent (8 to 12 percent of) that of the water content. Due to more abundant rhizomes, roots, and partially decomposed aerial parts in the first foot of soil the organic content is usually about 50 percent greater than it is in the next lower foot of soil. This relation does not obtain, however, in the saline marsh of the Popich transect (Table 11). In this marsh there was much more silt and clay in the first 6 inches of soil than in the soil below. This is undoubtedly due to frequent baths of detritus-laden water driven in by onshore winds. It is probable that the low organic content of the first foot of soil is due to the relatively greater amount of silt and clay therein. Despite the above facts there is an abundance of roots and rhizomes to a depth of 2 feet or more and numerous roots to a depth of 5 feet. This was true even under honey mangrove where no grasses whatever were present and where there probably had been none for several years.

SALT TOLERANCE

On the basis of the salinity of the soil water our swamp and marsh dominants may be arranged in four salinity groups (Table 12). The species of the first group, including two swamp and three marsh species were never found except in purely fresh water. They are the true halophobes of our region. Usually included in this group by most investigators are all those plants listed in the second group. It will be noted, however, that although they may grow in purely fresh water and may even be characteristic of fresh water marshes or swamps they do tolerate a considerable amount of salt.

There are several species of interest in the second group. Bald cypress, codominant with tupelo gum in fresh water swamps throughout the South, is accompanied by swamp maple and water ash into the slightly brackish areas but it leaves these species to venture into still more brackish water where its only woody companion is the red bay. Ghost forests of bald cypress are numerous in the Lake Pontchartrain-Lake Borgne region where this forest borders the saw grass marsh. There has been considerable speculation as to the cause of the destruction of these trees. All the available evidence points to salt water, brought inland by the historic hurricane in 1915, as the

TABLE 12. RELATIVE SALT TOLERANCE OF THE IMPORTANT SPECIES IN THE MARSH TRANSECTS STUDIED

SPECIES	Percent salt
STRICTLY FRESH WATER SPECIES	
Mikania scandens	(0.0)
Myriophyllum proserpinacoides	(0.0)
Nyssa aquatica	(0.0)
Panicum hemitomon	(0.0)
Piaropus crassipes	(0.0)
FRESH OR NEARLY FRESH WATER SPECIES	
Achyranthes philoxeroides	(0.0 – 1.48)
Castalia odorata	(0.0 – 0.2)
Cephalanthus occidentalis	(0.0 – 0.89)
Crinum americanum	(0.21 – 0.53)
Iris virginica	(0.21 – 0.53)
Mariscus jamaicensis	(0.0 0.2)
Nyssa biflora	(0.21 – 0.53)
Persicaria punctata	(0.0 – 0.89)
Pontederia cordata	(0.0 – 0.89)
Sagittaria lancifolia	(0.0 0.89)
Scirpus californicus	(0.0 – 1.13)
Taxodium distichum	(0.0 0.89)
Typha angustifolia	(0.0 – 1.68)
Typha latifolia	(0.0 – 1.13)
Utricularia macrorhiza	(0.0 – 0.53)
Zizaniopsis miliacea	(0.0 – 0.89)
BRACKISH WATER SPECIES	
Aster tenuifolius	(0.55 2.30)
Baccharis halimifolia	(0.0 – 1.98)
Borrichia frutescens	(0.87 – 4.43)
Convolvulus repens	(0.45 – 2.04)
Distichlis spicata	(0.45 – 4.97)
Fimbristylis castanea	(0.23 – 1.93)
Ipomoea sagittata	(0.23 – 2.04)
Iva frutescens	(0.21 – 1.98)
Juncus Roemerianus	(0.12 – 4.43)
Kosteletzkya virginica	(0.21 – 1.80)
Lythrum lineare	(0.55 – 1.68
Panicum virgatum	(0.21 – 2.04)
Phragmites communis	(0.0 2.04)
Scirpus Olneyi	(0.55 – 1.68)
Scirpus robustus	(0.64 – 3.91)
Solidago mexicana	(0.18 – 1.93)
Spartina cynosuroides	(0.55 – 2.04)
Spartina patens	(0.12 – 3.91)
Vigna repens	(0.23 1.26)
SALT WATER SPECIES	
Avicennia nitida	(3.68 – 4.97)
Batis maritima	(1.33 – 4.97)
Spartina alterniflora	(0.55 4.97)

destructive agency. Saw-grass is usually considered a fresh water species by most investigators. The writers have never found it in other than faintly brackish areas, except as relicts in areas from which salt water has been excluded. It is usually accompanied by white water-lily and bladderwort, both of which are typical of fresh water ponds. Cut-grass is a species which inhabits shallow canals or bayous, open cypress-gum swamps or forms a fringe of varying extent along the borders of dense stands of this community. It

is an unfailing companion of bald cypress in all its habitats and apparently is a good site indicator for the cypress-gum associes.

The list of species in the third group (Table 12) includes no trees or important fresh water species but does include practically all the important brackish marsh species. Even in this group several species occur which may be found growing in purely fresh water areas. Of these, *Achyranthes philoxeroides, Baccharis halimifolia, Phragmites communis, Samolus floribundus,* and *Typha angustifolia* may be found in fresh water habitats and it is here that they attain their best development. In the less saline of the brackish marsh transects the great "wet prairie" borders directly on the cane zone but in most brackish and salt marshes a salt grass zone is interposed between the cane associes and the marsh proper. With the exception of the honey mangrove community, which often replaces salt grass, the greatest salinity of the marsh grasslands is attained in the salt grass zone (up to 4.4 percent of salt). In the brackish marshes couch grass is the dominant *par excellence.* By virtue of its considerable size (up to 5 feet), its bunch grass form, its tremendous vigor and great range of salt tolerance this species is able to drive out most of its competitors. In more saline areas its size and vigor decrease and it shares dominance with black rush and salt grass. In still more saline areas it is entirely eliminated, largely in favor of salt cane.

The last group includes the true "salts" of the marsh grasslands. Honey mangrove and glasswort, which clan together on the bayou ridges, have been found in no other marsh area. Furthermore salt cane is of little importance in any other marsh but here constitutes more than 75 percent of the total vegetation and becomes of great importance in extending the land seaward in the saline habitat.

A casual inspection of the species list (Table 12) shows that most species have a wide range of salt tolerance. The narrowest range occurs in species whose upper limit of salt tolerance is very low. From this it may be inferred that the more salt a plant tolerates the greater its probable range. A probable exception to this rule is shown by the range of honey mangrove which thrives typically only in saline areas. In general typical brackish and saline species grow readily and much larger in somewhat fresher areas. Notable examples are couch grass and salt cane. In slightly brackish marshes (Bayou Villars transect) couch grass blooms at a height of 50 to 60 inches whereas in saline habitats (Yellow House transect) it is less than 18 inches high. In brackish marshes, especially in ditches, the flowering stalks of salt cane are 60 to 80 inches high whereas in saline marshes (Popich transect) they are less than 20 inches in height. It has been observed also that under conditions of high salinity plants are larger and healthier at higher elevations and along the shores of bayous, possibly due to better aeration obtaining under such conditions. Notable for their extreme ranges in salt tolerance are couch grass, black rush, salt grass, and salt cane. These species

are all major dominants in the brackish and saline areas, and probably aggregate 75 percent of the total vegetation in these marshes.

In only one report on salinity of marsh soils (Harshberger, 1911) that the writers have seen have determinations of salinity of soil water been made. In Harshberger's work samples were taken at various times at three localities near Belmar, New Jersey, but apparently not in any definite chronological sequence. Although he gave only the hydrometer reading we have converted these into percentages of salt at 15°C. in order to compare them with our results. In converting, a probable error as great as 0.2 percent is introduced but in spite of this his results parallel ours fairly closely. *Spartina alterniflora, Spartina patens,* and *Distichlis spicata* all have a range of salinity very similar to our determinations for these species and he states that the former two are very widespread and controlling in the New Jersey marshes. With Phragmites, Baccharis, and *Aster tenuifolius* there is a general agreement but he gives *Solidago mexicana, Spartina cynosuroides, Panicum virgatum* and *Typha angustifolia* a salt tolerance of less than 0.5 percent and classes them as fresh water species.

Visits to the New Jersey marshes and our experience and data indicate that his conclusions regarding these four species are quite untenable. It is probable that these data were founded on one or a very few determinations. In any event conclusions on ranges of salinity should be attempted only after the determination of many samples for one or more years or at least during the growing period of the community under investigation.

BIOTIC FACTORS

Of the biotic factors influencing the vegetation man is the most important. Many fresh water marshes have been reclaimed to make the richest of agricultural lands. This is effected by pumping the water from a system of canals into a leveed bayou. In many cases these reclamation projects have been abandoned due to insufficient or improper financing. Since the land sinks when it is drained the original marsh reverts to an open water area one to four feet deep when the projects are abandoned. Even in brackish marshes the land may be reclaimed, usually for sugar cane or rice production, as for example near the Foster transect, where a large portion of the marsh was formerly under rice cultivation. In certain cases the drained areas have never been used for crop production. In such marshes the vegetation develops rapidly, through stages quite unlike those in the natural sere, to a more mesic type. In addition to the drainage projects there has been a tremendous development of navigation canals. These have served to promote rapid run-off and also to bring about abnormal fluctuations in water level and salinity due to storms and tidal action.

Another important influence of man on the marshes is through the medium of fire. It is the practice of muskrat trappers to fire the marshes an-

nually just prior to or during the trapping season. This is done to make walking less laborious, to find traps more readily, and to improve the musk-rat food. There is some question on this last point but it is known with certainty that couch grass is adversely affected by fire and gives way largely to the three-cornered rush and bayonet rush, considered the best of the muskrat food plants. Fire, by removing the stalks of the previous year, decreases the amount of organic matter returned to the soil and thus impedes the elevation of the marshes. If the marsh is fired when the soil is wet in the absence of wind, little damage is done and a considerable fire hazard is removed. But in periods of extended drought, especially where the area is dissected by canals, the peaty humus, usually from one to three feet in thickness, becomes very inflammable and, when fired, burns furiously. This results not only in the destruction of both active and dormant plant parts, and the production of possibly injurious alkali but also in a lowering of the marsh level, and therefore, a reversion to a more hydric community in the sere.

Muskrats injure plants by feeding on their rhizomes, and in the making of burrows and houses. Around many of the houses the marsh is partially denuded for a radius of several feet and in most of these areas bayonet rush is abundant. Several mesic species, typical of higher communities but not found elsewhere in the marsh, grow on the muskrat houses. In addition, two spike-rushes (*Eleocharis* spp.), and bayonet rush, are especially abundant in areas partially denuded by muskrats. At present it is impossible to estimate the effects of muskrat activity on marsh vegetation but it would not be surprising to find that it modifies considerably the marsh composition and development. In heavily brackish areas fiddler crabs, horse mussels, and certain snails are very abundant but their effect on the vegetation is not obvious. The direct effect of the ubiquitous salt marsh mosquitoes is also of no importance but their indirect effects are far-reaching. In many areas they have impeded the ecesis of man, thereby reducing greatly the destructive activities of this major biotic factor and tending to preserve the marshes in their primeval condition.

PHENOLOGY OF THE MARSHES AND ASSOCIATED COMMUNITIES

Phenological data were obtained throughout an annual cycle by monthly trips to the seven areas under investigation. In the case of all plants the stage of development, the conditions of buds, the stage of flowering, the presence and condition of fruit, and time of dissemination of seeds were carefully observed and entered in tabular form in field notebooks. Symbols or combinations of symbols for the phenological stages were devised and monthly records were kept for each species by the aid of these symbols. It should be stated that it was often impracticable to return to the areas ex-

actly one month following previous visits. Because of this the authors are unwilling to postulate the exact periods of anthesis of particular species at any one station. It is believed, however, that the community data supplied in Figs. 14, 15, and 16 represent typical conditions for our marsh vegetation.

In Louisiana blooming plants are usually found during every month of the year. This is especially true in forest communities where certain of the trees start their anthesis in January. Certain of the species (*Pontederia cordata, Piaropus crassipes, Sagittaria lancifolia,* and *Vigna repens*), may bloom for 8 months or even more although some species have a flowering period of less than 3 weeks. Certain other species may have one blooming period in the spring and one in the autumn. Foremost among these are *Sambucus canadensis, Berchemia scandens, Cerothamnus ceriferus, Iva frutescens. Solidago mexicana, Spartina patens, Distichlis spicata, Zizaniopsis miliacea,* and *Aster tenuifolius.*

Because of the mild winters and exceptionally long growing period (326 days) the seasonal aspects do not correspond in chronology or duration to those usually indicated in textbooks of ecology. The prevernal period, comprising the month of February and the early part of March, is ushered in by the blooming of species in the shrub and cane communities. These include *Carex lupulina, Hydrocotyle verticillatus, Cerothamnus ceriferus, Rumex verticillatus,* and the conspicuous butterweed *(Senecio glabellus).* Compared to the vernal aspect, which includes most of March and the month of April, the prevernal phase is characterized by meager anthesis. More species begin flowering in the vernal aspect than during any similar period of the year. In the same aspect the anthesis of the true marsh species is inaugurated (Figs. 14, 15). Important among these are giant bulrush and maiden cane *(Panicum hemitomon)* of the fresh water marsh; and bayonet rush, black rush, and couch grass of the brackish marshes. The estival aspect (May, June, July), begins with a month of reduced activity but enough new species initiate flowering in the fresh water, nearly fresh, and moderately brackish marshes to produce a maximum number of flowering species before the end of the aspect.

Several vernal and still more estival species continue in bloom throughout August and September (autumnal aspect). A goodly number of species initiate flowering during the autumnal aspect especially in the heavily brackish and saline marshes (Fig. 16). Conspicuous during this phase are the cottony heads of buckbrush, the yellow clusters of the seaside goldenrod *(Solidago mexicana)*, the nodding plumes of roseau, the strict panicles of salt cane, and the numerous blue and white heads of salt-marsh asters. A few prevernal and a progressively smaller number of estival and autumnal species continue to bloom during October and November. In the marshes alone there were sixteen species in flower during October and ten species in November. Since no new species inaugurate anthesis during these months it is deemed im-

proper to assign this period to the autumnal aspect. We are, therefore, designating these months as the postautumnal aspect. During this aspect there is a gradual deterioration of the vegetation which is hastened by progressively colder weather. The leaves of the grasses and sedges dry in place with a rapid change to tans and browns. These become the dominating colors of the marsh panorama and are broken only by the green of the buckbrush and marsh elder. Since there is little or no anthesis during December and January in true marsh communities this period is logically labelled as the hiemal aspect. But all is not inactivity; the shoots of Hydrocotyle, Rumex, Senecio, Scirpus, Sagittaria and many another plant are vegetating as early as late December and are well advanced before the prevernal aspect is introduced in February.

In the cypress-gum swamps species are in bloom throughout the year since the bald cypress initiates anthesis in late December or January and swamp maple, black willow and wax myrtle *(Cerothamnus ceriferus)* begin flowering in January. There is then no true hiemal aspect in the forest communities. In general anthesis is inaugurated first in the oak forest and progressively later in the cypress-gum swamps, shrub zones, cane communities, fresh water marshes, nearly fresh, brackish, and saline marshes. Although flowering in the above communities is initiated in the above order it is terminated in approximately the reverse sequence. Despite the fact that the general onset of anthesis is later in the more brackish areas the blooming of a given species is usually earlier the more saline the habitat.

In general more species were found to flower in spring (April-May) and early autumn (August-September) although several communities are characterized by a summer (June-July) maximum. The cypress-gum swamp, in fresh water areas, exhibits a characteristic spring (April-May) and a lesser autumn (September-October) maximum. But the cypress-gum swamp in faintly brackish habitats is characterized by a summer (June-July) peak only (Fig. 15). In the oak forest there are more woody plants in bloom in the early spring (April) than in any other aspect but in the brackish cypress-gum swamps the peak is not reached until June. Since the herbaceous population also reaches its flowering crest during June the complete graphs for the brackish swamps display notable summer maxima.

Only two examples of the shrub community (Baccharis-Iva associes) were studied. Both of these exhibited characteristic spring (April-May) and autumn (August-September) peaks. This is of interest since the more brackish community on Grand Bayou possesses only one-third as many species as the shrub zone at Oak Island. The cane community (Phragmites-*Spartina cynosuroides* associes) usually includes few species since both of the large canes are very vigorous and readily oust their competitors. Despite this relative paucity of species they show unmistakable vernal (April) and autumnal (September) peaks. The salt grass community (Distichlis con-

socies) is well developed only in the more brackish and saline areas. It is also characterized by a scarcity of species, fourteen being the greatest number encountered in any one of these communities (Fig. 16). Of the four examples studied all exhibit an autumnal maximum in anthesis. There may be a less prominent rise in July but there are few vernal species. The marshes proper differ considerably in their phenology (Figs. 14, 15). The relatively fresh water marshes, as well as the less salty of the brackish marshes (in Bayou Villars and Oak Island transects), have the greater number of species in bloom during the estival (June-July) aspect, whereas the more brackish and saline ones are characterized by autumnal (August-September) maxima.

UTILIZATION OF THE MARSHES

Under natural conditions the marsh habitats afford a great variety and quantity of animal life of considerable value to man. The marshes include especially a great diversity of bird and aquatic life. Not only are they the home of many resident game girds but they also constitute the winter home of a majority of ducks, geese and other waterfowl which nest in North America east of the Rockies. Because of this fact the problem of the preservation of these marshes has attracted state, national, and even international attention. Perhaps the best known marsh animal is the Louisiana muskrat which thrives best in the brackish habitat. Of the aquatic life proper there is an abundance of shrimp, fish, and other organisms in the innumerable bayous, lakes, and lagoons which are present in these areas. The value of these natural resources is measured not only in the economic return but also in the incentive which they give for healthful outdoor sport, recreation, and education.

It has been estimated by Viosca (1928) that the money value of these natural resources aggregated over twenty million dollars in 1924-1925. Of the marsh animals the muskrat is the most important having contributed a product worth six and a half million dollars. The balance of the revenue came largely through the sale of shrimp, crabs, fish, oysters, frogs, turtles, and alligators. Of the plants the three-cornered rushes, which furnish the best muskrat foods, are the most important economically but some of the grasses such as couch grass and salt grass furnish pasturage for cattle which wade out into the marshes to feed. In addition couch grass is utilized in broom-making since it is green when properly cured and requires less labor than broom corn in broom manufacture. Revenue also is derived from the army of pleasure seekers and sportsmen who visit the marshes yearly and who contribute largely to the support of numerous guides and resort keepers. The Louisiana marshes still constitute a mecca for the hunter, fisherman, and nature-lover. Since the marsh areas are the home of a remarkable variety of plants, fish, frogs, and birds they serve to attract many stu-

dents and nature-lovers. In addition a number of species exist here which are used in educational institutions throughout the world.

Many of the marshes, especially in the salt water habitats, still retain their primitive status, but many of the "wet prairies" have been much modified by fire, canalization, and drainage. When the water level is lowered a few inches the land is suitable only for grazing. But when the level is lowered still further by means of a system of levees and pumps the land is fine for the production of corn, rice, and even sugar cane. There are many thousands of acres in the fresh water region west of the Mississippi that have been drained to make suitable agricultural land. A notable development is the area between Raceland and Houma. Unfortunately the heavy overhead for flood protection and drainage has caused the failure of many of these reclamation projects. Since drainage destroys valuable natural resources without producing benefits proportional to the reclamation costs it is probable that further reclamation should not be attempted in the near future in the marshes of southeastern Louisiana.

SUMMARY

1. *Scope of investigation.*
   a. This investigation deals with the composition, development and phenology of plant communities in marshland areas and with the causal factors in the distribution of the component species.
   b. The work reported in this paper extended over a period of four years. It involved 23 reconaissance trips, 66 routine studies made in seven transects during one annual cycle and about 20 confirmatory trips subsequent to the routine investigation.

2. *Areas studied.*
   a. The region is one of little relief but the streams are flanked by natural levees, which slope gradually away from the stream front to paludal basins, in which the soil surface is usually covered with water.
   b. Each transect was so established as to include all the communities on the elevations and a considerable portion of marsh proper in the paludal basin.
   c. Of the transects studied in detail one was located in a fresh water area, a second was in a nearly fresh area (less than 0.5 percent salt); three were located in brackish areas (0.5 to 2.0 percent salt) and two were in saline areas (2.0 to 5.0 percent salt).

3. *Communities in the transects.*

In the transects studied the writers recognized 11 distinct communities of which three are forests, four are zonal communities in which the average water level is below the soil surface, and four are true marshes in which water usually stands on the soil.

   a. In the strictly fresh water area (Raceland transect) an oak forest (Quercus association) is bordered at lower elevations by the cypress-gum swamp (Taxodium-Nyssa associes) in which bald cypress and

tupelo gum are the dominant species. A forest fringe in which black willow and cut-grass are the conspicuous species, separates the cypress-gum swamp from a vast marsh (Typha-Scirpus associes) in which giant bulrush and broadleaf cattail account for the bulk of the vegetation.

b. In the nearly fresh habitat (Slidell) a forest of loblolly pine is fringed on the marshward side by cypress-gum swamp (Taxodium-Nyssa associes) in which swamp black gum is substituted for tupelo gum. The cypress-gum swamp borders directly on the saw-grass marsh (Mariscus consocies) which consists mainly of saw-grass.

c. In the slightly brackish transect (Bayou Villars) the cypress-gum swamp (Taxodium-Nyssa associes) includes bald cypress as the sole dominant. Here the cypress swamp abuts directly on a brackish marsh (Spartina-Distichlis-Juncus associes) which includes one major dominant, couch grass. This marsh is the most cosmopolitan of all since it embraces both fresh and brackish water species.

d. In the moderately brackish transect (Oak Island) the oak forest is fringed at progressively lower elevations by shrub, cane, and true marsh communities. The shrub belt (Baccharis-Iva associes) is characterized by a predominance of marsh elder. The cane zone (Phragmites-*Spartina cynosuroides* associes) is distinguished by a single dominant, quill cane. The brackish marsh (Spartina-Distichlis-Juncus associes) is a uniform, extensive "wet prairie" including couch grass and salt grass as the dominant species.

e. The strongly brackish habitat (Foster transect) embraces cane, salt grass, and brackish marsh communities at gradually decreasing elevations away from the bayou. The cane zone (Phragmites-*Spartina cynosuroides* associes) comprises *Spartina cynosuroides* as the major dominant and *Phragmites communis* and *Panicum virgatum* as minor codominants. In the salt grass belt (Distichlis consocies) salt grass, Distichlis spicata, forms a nearly continuous stand. Of the species in the marsh proper (Spartina-Distichlis-Juncus associes) salt grass and black rush are the predominant species.

f. Of the two transects in saline areas, the one of lower salinity is the Yellow House transect. Here the bayou ridge, underlain by oyster shells, supports a shrub community. This is paralleled at successively lower levels by cane, salt grass and true marsh communities. The shrub, cane, and salt grass communities are not conspicuously different from those previously described except for a notable paucity of species. The saline marsh (*Spartina alterniflora* consocies), also characterized by a scarcity of species, is almost entirely composed of salt cane and black rush.

g. In the most saline habitat (Popich transect) the bayou front is populated by the unique honey mangrove, which is the sole dominant of the Avicennia consocies. This is paralleled, away from the bayou, by a salt grass zone (Distichlis consocies) in which salt grass is the predominant species. The body of the area is a saline marsh (*Spartina alterniflora* consocies) in which salt cane accounts for most of the vegetation.

4. *General vegetational relations.*
   a. The fresh water areas, including strictly fresh and nearly fresh habitats (less than 0.5 percent salt), are characterized by the presence of a cypress-gum swamp and a marsh of tall sedges and grasses from 8 to 12 feet tall. The salt water areas, including brackish and saline habitats (0.5 to 5 percent salt) are distinguished by the absence of the cypress-gum swamp, the presence of zonal communities, and a marsh of small grasses, sedges, and rushes from 2 to 4 feet in height.
   b. In the salt water habitats three zonal communities (shrub, cane, and salt grass zones) often occur on the bayou ridges above the level of the marsh proper. These four communities may be found on a slope having a fall of less than one foot. Therefore the transition from one community to another may be conditioned by a change in elevation of less than 3 inches.
   c. The dominants of the fresh water marshes include broadleaf cattail, narrowleaf cattail, giant bulrush and sawgrass. The dominants of the salt water marshes are: couch grass, black rush, salt grass and salt cane. These species account for the bulk of the marsh vegetation and constitute the great "double quartet" of the marshes of southeastern Louisiana.

5. *Edaphic factors.*

Of the habitat factors the water level and salinity of the soil water appear to be the most important, although soil moisture (and possible organic matter) may be influential locally or during unfavorable periods.

   a. Salinity.
      (1) Individual determinations of salinity fluctuate widely with season and weather; comparisons are therefore made on the basis of year-round averages.
      (2) Free soil water in marsh communities is usually more saline than the surface water of the marsh, that of adjacent lagoons, bayous, and lakes.
      (3) In a given area the highest salinity is usually found in a community where the average water level is close to the soil surface.
      (4) The higher the land level, the lower is the salinity of the soil water. (This is true for all elevations except the first few inches above the adjacent open water.)
      (5) Strikingly different types of marshes are found in strictly fresh, nearly fresh, brackish, and saline areas.
      (6) With increasing salinity, marsh dominants and several other plants are progressively stunted.
   b. Water level.
      (1) Depth of water in the marsh proper is greatest in fresh water areas; it decreases progressively with increasing salinity.
      (2) Aquatic communities are present in fresh water bodies but are lacking in salt water lagoons.
      (3) The greater the salinity, the higher is the elevation at which most species grow. (The true halophytes are exceptions.)

(4) In salt water habitats several plant communities are found where the mean water table is near or below the soil level.

c. Water content and organic matter.

(1) Water content and percentage of organic matter in the soils are lowest in the pine and oak forests, and successively higher in the shrub, cypress-gum, cane, and salt-grass communities.

(2) In the marshes proper the water content is relatively low (absolute minimum 98 percent) in the fresh water and saline marshes and progressively higher (absolute maximum 867 percent) toward the brackish marshes.

(3) In the marshes proper the organic content is relatively low in fresh water and saline marshes but very high (59 percent) in the brackish marsh.

(4) In general the amount of organic material in the upper 12 inches of soil is approximately 50 percent greater than it is in the next lower foot of soil.

d. Salt tolerance.

(1) On the basis of relations to salinity the plants of swamp and marsh communities may be divided into halophobes (fresh water only), facultative halophytes, and true halophiles (salt water only). Certain plants have a narrow range of salt tolerance but most of the species range widely.

(2) In probable order of salt tolerance the major marsh dominants are: *Mariscus jamaicensis, Scirpus californicus, Typha latifolia, Typha angustifolia, Spartina patens, Juncus roemerianus, Spartina alterniflora*, and *Distichlis spicata*.

e. Of the bitoic factors man is of greatest importance due to his activity in canalization, reclamation projects and periodic firing of the marshes.

6. *Phenology*.

a. Six stages are recognized as follows: *pre-vernal* (February and early March); *vernal* (most of March, all of April); *estival* (May, June, July); *autumnal* (August, September); *post autumnal* (October, November); *hiemal* (December, January).

b. The total period of anthesis in true marsh communities is usually about 10 months, but in forest communities it may include every month of the year.

c. Certain species bloom continuously for 8 months, others, less than 3 weeks; still others exhibit two blooming periods, usually in early spring and late autumn.

d. The number of species in flower is small during the pre-vernal period; it increases rapidly during the vernal aspect, and reaches a maximum during the estival aspect. It attains a secondary peak in the autumnal aspect, but declines gradually during the post-autumnal period to scattered specimens or none in the hiemal aspect.

e. The maxima of anthesis in the marshes proper are estival; those in the zonal communities (shrub, cane, and salt grass belts) are vernal and autumnal.

f. The initiation of blooming, for the greatest number of species, occurs in the vernal aspect, although there is a secondary peak in the autumnal period. In general the onset of anthesis is earlier in the zonal communities than in the true marsh associes.

g. The greater the salinity of a marsh, the later is the onset of anthesis for the majority of its species and the later is the maximum anthesis of the community. However, each individual species tends to bloom *earlier* in the more saline parts of its range.

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CHARACTERISTICS OF MAJOR GRASSLAND TYPES IN WESTERN NORTH DAKOTA[1]

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CONTENTS

CHARACTERISTICS OF MAJOR GRASSLAND TYPES IN WESTERN NORTH DAKOTA

INTRODUCTION

Knowledge of variation in botanical composition of grassland, as well as the causes and consequences of the variation, is basic to scientific land management. Striking differences in vegetation are characteristic of the badlands along the Little Missouri River in western North Dakota (Fig. 1). Some of the conspicuous vegetation types are mixed prairie on uplands, little bluestem on hillsides, saltgrass and sagebrush on stream terraces, sandgrass on hills, and woodland along stream courses. Following preliminary observations in 1932 and 1933, detailed study was started in 1934 and continued at greater length in the more favorable season of 1935. The objects were to determine the composition, frequency, and abundance of species in several examples of different types, to study soil and other conditions in each, and to classify the areas studied into types on the basis of data collected.

This study was conducted chiefly in the vicinity of Sentinel Butte and Medora in western North Dakota, in an unglaciated section of the northern

FIG. 1. View of Little Missouri Region about 16 miles southeast of Sentinel Butte. Trees are mostly ash, with Symphoricarpos, Rosa, Ribes, and Prunus between; dark areas on slopes little bluestem type; light areas on slopes western wheatgrass-grama-sedge type, sagebrush in valley of Garner Creek in middle distance at left, and grama-needlegrass-sedge type on plateau tops. August 31, 1935.

plains. The elevation was 2,000 to 2,600 feet for most of the test areas. The soils had developed from yellow and ash-gray shales, sandstones, and clays of the Fort Union formation of the Tertiary age or from alluvium derived from them. The Fort Union also contains numerous beds of lignite and baked shale and sandstone, called "scoria," produced by burning lignite beds. (Gauger et al, 1930.)

The soils of this region are in the Pedocal group according to Marbut's (1928) classification, and the general soil region is that of the dark-brown soils, which, south of the glacial boundary, are classified as the Rosebud series. The most important series in the Dark Brown Zonal Group are the Morton, in which the parent material is residual and the Farland, developed from general alluvium. The Patent, from local alluvium, and the Bainville from residual material are the light-colored immature soils associated with the more broken relief (Ableiter).

Due to erosion by wind and water and burning lignite veins there is great heterogeneity in topography, as plateau tops, slopes, terraces, valleys, buttes, low hills, and knobs of numerous shapes.

The mean precipitation is about 15 inches, (range 6-23) about 40 percent falling in May and June and only 12 percent during November to February, inclusive. The annual mean temperature is 41°F. July is the hottest month with a mean of 68.5°F. Prevailing winds are northwest (Roberts, 1935). The precipitation at the Olstad Ranch during the spring and summer of 1935 was: March, 1.02 ins.; April, 1.70; May, 2,25; June, 2.33; July, 3.33; and August, 1.12.

METHODS

Considerable time and care were devoted to selecting test areas which were sufficiently large, uniform in topography and vegetation, and free from harmful effects of grazing, mowing, and trampling. Usually the areas were located in winter-grazed pastures, in ungrazed portions of land adjoining cropped fields or in lightly grazed pastures. The test areas varied in size from about 2 to 20 acres. Homogeneity was considered of greater importance than size.

The frequency, abundance, and herbage cover of species were determined by the frequency-abundance and point methods (Hanson, 1935; Levy, 1933). In the former 30 m^2 sample areas and in the latter a total of 300 points were used in each test area. A total of about 900 square meter sample areas were used in this study. The data showing results of these botanical analyses are given in Tables 1 and 2.

A trench was dug in a carefully selected, typical place in each area after the vegetation had been studied. The soil profile and root system were examined and described from the sides of the trench. Samples of soil were taken from each horizon for laboratory analyses. Effervescence was tested in the

TABLE 1. Classification of 36 test areas into types and the frequency X abundance of chief species, 30m² quadrats for each test area. T—is less than 0.5, D—dominant, A—abundant, F—frequent, S—scarce. Test area 14* is similar to 15 and 17 but is transitional to Type 1 because of slightly higher elevation.

Species	TYPE 1 Bouteloua, Stipa, Carex							TYPE 2 Agropyron, Bouteloua, Carex				TYPE 3 Andropogon scoparius			TYPE 4 Calamovilfa				TYPE 5 Artemisia cana			TYPE 6 Distichlis, Agropyron			TYPE 7 Distichlis, Puccinellia		TYPE 8 Buchloe	TYPE 9 Andropogon furcatus					TYPE 10 Miscellaneous			
	1	2	3	4	6	7	36	10	11	12	13	25	26	31	21	22	23	24	18	19	20	15	17	14*	16	35	33	27	28	29	32	30	5	8	9	34
Bouteloua gracilis	95	100	95	100	95	91	D	100	75	100	100	3	2	S	47	13	28	28	75		48	15	65	95		A	S	1				13	74	100	100	D
Agropyron smithii	5	9	66	8	2	T	F	100	63	55	91	3	1	S	T	T		1	67	95	100	97	100	67	T		A	1	1		S	2	74	88	74	S
Stipa comata	98	79	46	70	95	29	D	1	6	16			T		44	30	42	26	2	2	1	1	1	64					T	T		3	56	57	71	S
Koeleria cristata	47	8	1	1		33			1	2		10	4	S	10	15	17	25						T				1	5	12	S	12	4	17	9	
Carex filifolia	49	100	65	28	71	T	F	97	66	85	78	23	3	F	84	43	55	16						7				T	1	T		4	11	8	27	
Carex stenophylla	59	9	25						2						1												S			53		T	28	19	14	
				36	13	67	A					14	8				54											12								
Carex pennsylvanica																86		93											47			51				
Andropogon scoparius						8						100	100	D	18	2		16										95	3.	70	F	6				
Calamovilfa longifolia	4			2		13						1	4	S	40	56	54	84											T			22				
Calamagrostis montanensis	12		1	11	8	2	F					T			1			T			T			5						T		1				
Andropogon furcatus						T																						95	100	100	D	46				
Distichlis stricta																						46	88	45	100	D										
Stipa spartea						3																							1			21				
Stipa viridula													T						48	4	50		8				S	T			S	2		2	2	S
Bouteloua curtipendula												9	8															22	1	5	F	1				
Puccinellia nuttalliana																									70	D										
Hordeum jubatum																									22											
Sporobolus heterolepis																																51				
Plantago purshii			1	3	T	1		25	45	2		T					T		2			1		1									23	T		
Draba nemorosa			T	2				13	6			T			1				2			2		T				T					10			
Artemisia cana																			29	90	24		1													
Juncus balticus																																8				
Buchloe dactyloides																											D									
Poa buckleyana																											S									A
Miscellaneous grasses	3	2	1		T	10		1		1	T	4	1		6	1	1	21	1	2	5	7		T	1			1	5	2	S	14	3	T	1	..
Miscellaneous forbs	65	29	25	40	22	39		16	16	9	4	28	13		15	7	16	12	5	5	19	22	2	36	15			28	41	24		40	23	4	11	
Total no. species 30m² quadrats	46	42	33	50	44	53		20	29	24	12	52	46		42	40	42	35	50	31	23	36	28	33	24			55	63	41		86	42	18	24	
Average no. species 30m² quadrats	17	10 9	12 3	19 2	11 5	16 9		10 3	11	6 8	3 7	12 8	10.8		12 6	9 9	10 7	10 2	12 9	6 1	5 2	7 9	5	9 2	6 6			13	17 1	12 2		20 3	13 8	6.1	7	

*Intermediate to Type 1 (See p. 89)

TABLE 2. Percentage of herbage cover of chief species and of bare ground in a total of 300 points for each test area, according to the point method. Same test areas as in Table 1.

Species	TYPE 1 Bouteloua, Stipa, Carex						TYPE 2 Agropyron, Bouteloua, Carex				TYPE 3 Andropogon scoparius	TYPE 4 Calamovilfa				TYPE 6 Distichlis Agropyron			TYPE 7 Distichlis, Puccinellia	TYPE 9 Andropogon furcatus		TYPE 10 Miscellaneous		
	1	2	3	4	6	7	10	11	12	13	25	21	22	23	24	15	17	14	16	27	29	5	8	9
Bouteloua gracilis	26	36	37	43	17	19	27	23	32	47		8	4	5	6	5	22	31				29	53	50
Agropyron smithii	3	4	12	1			30	35	31	28			T		T	59	45	23				28	20	25
Stipa comata	25	20	15	19	22	7		3	2			16	7	17	5		T	20			T	12	7	11
Koeleria cristata	6					9					2		2	3	4						3		1	T
Carex filifolia	10	22	16	1	12	T	22	12	17	17	8	11	6	7	2			1				5	6	
Carex stenophylla	13	4	6					6													12	7	7	3
				14	10	27					4			19						17				
Carex pennsylvanica													27		27									
Andropogon scoparius						3					49	3								13	17			
Calamovilfa longifolia						14						33	42	34	45									
Calamagrostis montanensis	3																							
Andropogon furcatus																				53	58			
Distichlis stricta																13	22	10	52					
Stipa spartea						3																		
Stipa viridula																	3						T	
Bouteloua curtipendula											6										3			
Puccinellia nuttalliana																			27					
Hordeum jubatum																			6					
Miscellaneous grasses		1	1	2	4	2		1	1		1	10	1	1	3	1	1			5	T	2	T	1
Miscellaneous forbs	10	3	3	15	9	8	8	8	1	1	8	6	3	5	3	11	1	2	5	10	4	7	2	1
Bare ground	4	10	10	5	26	8	13	12	16	7	22	13	8	9	5	11	6	13	10	2	3	10	10	3
Total hits of vegetation	410	450	425	490	340	564	392	436	392	334	296	413	436	465	439	274	402	432	455	555	429	495	359	472

field with dilute HCl solution. Complete profile descriptions were made for each area but only a few typical ones are included in this paper.

Mechanical analyses of the soil samples were made by the Bouyoucos hydrometer method (1935). In many of the analyses sodium silicate was used as a deflocculating agent (Thoreen, 1933). Classification and terminology of soil texture are those used by the Bureau of Chemistry and Soils as described by Davis and Bennett (1927). Moisture-holding capacity was determined by the use of Hilgard soil pans (Duggar and Helgeson, 1933).

Total soluble salts were determined by the use of an electrolytic bridge, essentially similar to that described by Davis (1927). Soil reaction was determined electrometrically by means of the quinhydrone electrode for pH values up to 8.0 (Snyder, 1935), while above this cresol red and thymol blue were used as indicators in the colorometric method. The soil extract was obtained by the use of a sodium chloride leaching solution described by Morgan (1932).

Loss-on-ignition procedure followed Wright (1934), carbonate determinations according to Mehlich et al (1933), and tests for water-soluble nitrate nitrogen, phosphorus and chloride and exchangeable potassium, calcium, and sodium, according to procedures described by Morgan (1935).

The results of the soil determinations are presented in Table 3.

DESCRIPTIONS OF TEST AREAS

Each of the test areas is briefly described because variations occur between any pair that may be selected. The most accurate classification of vegetation is dependent upon comparing differences and similarities of selected areas which are studied in detail. The areas which show sufficient similarity to one another in essential characteristics are then naturally classified in one group. The differences between individual test areas are important in showing the variation within a group. The individual areas are also of importance in indicating that land use management must be based upon characteristics of individual areas, and not only upon generalized types. It is one of the duties of ecological research to describe these variations and to show how scientific classifications of vegetation must be based upon qualitative and quantitative data.

TEST AREA NUMBER 1 (JUNE 16, 1935)

This test area was located on a gentle, upland, south-facing slope, 10 miles northwest of Sentinel Butte in T. 141, R. 104. The dominants were Bouteloua, Stipa, and Carex. As indicated by the topography and by the sandstone and scoria particles in the parent material, the soil has developed from material eroded from former buttes or hills. This area is typical of much land cropped to wheat.

DESCRIPTION OF A TYPICAL UPLAND PROFILE IN MORTON FINE SANDY LOAM

Inches	
0- 1	Dark brown, fine sandy loam forming fine, crumb-like mulch. Very few roots.
1- 7	Dark brown, fine sandy loam. Coarse, friable crumb structure. Grass roots very numerous.
7-17	Brown, fine sandy loam distinctly lighter in color than the above horizon. Coarse, blocky structure breaking into angular fragments up to 1 x 2 x 0.5 inches.
17-20.5	Transitional horizon, light brown, fine sandy loam, effervescing[1] moderately.
20.5-32	Light brown, fine sandy loam becoming lighter colored with depth. Digs out in coarse angular fragments, readily friable. Effervescence moderate. Roots numerous but decreasing.
Below 32	Parent material. Light grayish brown, fine sandy loam with particles of sandstone and scoria intermixed, in the upper part somewhat cemented with carbonates which occur in streaks and blotches throughout. Effervescence strong. Roots of *Carex filifolia* more numerous in the parent material than those of other species. Roots decreased rapidly below 32 inches to working depth at 40 inches.

On June 16 the moisture of recent rains had penetrated to 32 inches. It was dry below.

The scarcity of *Agropyron smithii*, the presence of Calamovilfa, the abundance of Bouteloua, Stipa, Koeleria, *Carex* spp., and forbs; the high number of species (46) found in the test area and per quadrat (average of 17) appear to be associated with the uniform sandy loam soil which permitted excellent moisture penetration and root development to a working depth of 40 inches, freedom from salinity, absence of shallow carbonate layer, and the friable structure and dark brown color of the well-developed solum which extended to a depth of 20.5 inches. Vegetation development and soil development were apparently nearing maturity. Factors responsible for this development were freedom from continued overgrazing, cultivating, excessive mowing, and serious erosion.

TEST AREA NUMBER 2 (JUNE 18, 1935)

Test area number 2, typical of old uplands which are under cultivation, was located on a nearly level plateau top 7 miles east of Medora (Sec. 31, T. 140, R. 100). The dominants were Bouteloua, Carex, and Stipa. The soil, Morton fine sandy loam type, had developed from parent material residual from sandstone.

The abundance of *Bouteloua gracilis, Stipa comata, Carex filifolia,* and the forbs; the scarcity of *Agropyron smithii;* and the fairly large number of species in the area appear to be associated with the well developed solum which was brown in color, 23 inches deep and with structure favorable to

[1] Effervescence in soils indicates the presence of free $CaCO_3$.

root growth; sandy loam texture in both solum and parent material; level topography which reduced runoff and erosion to a minimum; and freedom from excessive salt concentration. Both soil and vegetation were mature or nearly so. The deeper solum, the absence of *Calamagrostis montanensis* and Calamovilfa, and the more pronounced carbonate layer indicate that this test area was more mature than number 1.

TEST AREA NUMBER 3 (JULY 27, 1935, FIG. 2)

This area was located on a fairly level plateau top, on the Olstad Ranch, about 15 miles southeast of Sentinel Butte (Sec. 5, T. 138, R. 103). The dominants were Bouteloua, Agropyron, Carex, and Stipa. The soil type was Morton clay loam.

The decrease in abundance and cover of *Stipa comata* and *Carex filifolia* in this area as compared with test areas 1 and 2, the increase in *Agropyron smithii*, the abundance of *Bouteloua gracilis*, and the shallower working depth of roots (30 inches) were associated with heavier soil (29.7 percent clay to working depth compared to 9.9 and 14.1 in areas 1 and 2), higher moisture-holding capacity, higher content of carbonates especially in the 14 to 24-inch layer, and a pronounced carbonate layer between 31 and 33 inches. Although

FIG. 2. Test area number 3, grama-needlegrass-sedge type on plateau about 15 miles southeast of Sentinel Butte. White fruiting stalks of *Stipa* comata are conspicuous against the darker background of *Bouteloua gracilis*, *Agropyron smithii*, and *Carex* spp. July 26, 1935.

runoff and erosion were negligible on this nearly level plateau, the solum was only 14 inches deep.

TEST AREA NUMBER 4 (AUGUST 3, 1935)

Test area 4 was located on a school section (state owned) in the gently rolling, upland prairie 4 miles west of Dickinson. The dominants were Bouteloua, Stipa, and Carex. The soil type was Morton sandy loam. Land of this kind is mostly under cultivation in this region.

The great variety of species (50 in 30 m^2 quadrats) and the dominance of *Bouteloua gracilis*, *Stipa comata*, and Carex were associated with soil texture mostly sandy loam, well developed solum to depth of 33 inches which was acid in reaction to a depth of 22.5 inches, deep carbonate zone at 45 to 50 inches, and freedom from excessive runoff and erosion. The shallow working depth of roots (28 inches) may have been caused by death of deeper roots due to droughts in recent years. The texture and color of the solum and the character of the vegetation are characteristic of approximate maturity of soil and vegetation. The high proportion of sand in this soil indicates that continuous cultivation may result in serious wind erosion.

TEST AREA NUMBER 5 (JULY 1, 1935)

This area was located on a fairly level, upper terrace about 10 feet above a creek, on the Olstad Ranch 16 miles southeast of Sentinel Butte (Sec. 4, T. 138, R. 103). The dominants were Bouteloua, Agropyron, Stipa, and Carex. The parent material was alluvium.

DESCRIPTION OF A TYPICAL PROFILE IN AN UPPER TERRACE IN GORHAM SANDY LOAM

Inches	
0- 2	Dark brown, sandy loam; loose and friable, mulch-like. Roots few. rhizomes numerous.
2- 7	Dark brown, sandy loam with coarse, angular fragmentary structure. Pieces are 1/2 to 3/4 in. in diameter, readily friable. Accumulation of scoria particles and yellowish chalky material occurs at the bottom of this horizon. Roots very numerous.
7-21	Light brown, clay loam streaked with organic matter above. Prismatic structure, moderately effervescent. Roots numerous.
21-30	Light yellowish brown, sandy clay loam. Blocky structure, soil falling out in irregular angular pieces, readily friable. Effervescence moderate, roots very numerous.
30-33	Light brown, clay. Nearly structureless, very hard, streaked and mottled with carbonates. Moderately strong effervescence, most roots end here.
33-38	Dark brown, silty clay. Soil falling out in vertically elongated pieces up to 3 inches. Effervescence moderate, dead roots rather numerous. Carbonate flecks numerous. Probably represents a buried soil horizon.
38-59	Light olive gray, alternate layers of clay and fine sand, effervescing moderately with HCl. Carbonate region conspicuous at 55 inches. Roots become scarce at 59 inches. Working depth of roots is 28 inches.

The heterogeneity of the soil is pronounced, varying from sandy loam to clay, from a carbonate content of 7.7 percent in the surface 2 inches to 20.8 percent at 38 to 59 inches, total soluble salts from 428 p.p.m to 6,300. In addition the profile shows a former surface layer at 33 to 38 inches. The present solum is only about 7 inches deep. The vegetation on this heterogeneous and youthful soil was characterized by the abundance of *Agropyron smithii* and *Bouteloua gracilis*, the presence in much smaller numbers of *Stipa comata*, Carex and *Koeleria cristata;* fairly large numbers of *Plantago purshii* and *Draba nemorosa;* and a fairly high total number of species. Frequently land similar to this area is under cultivation.

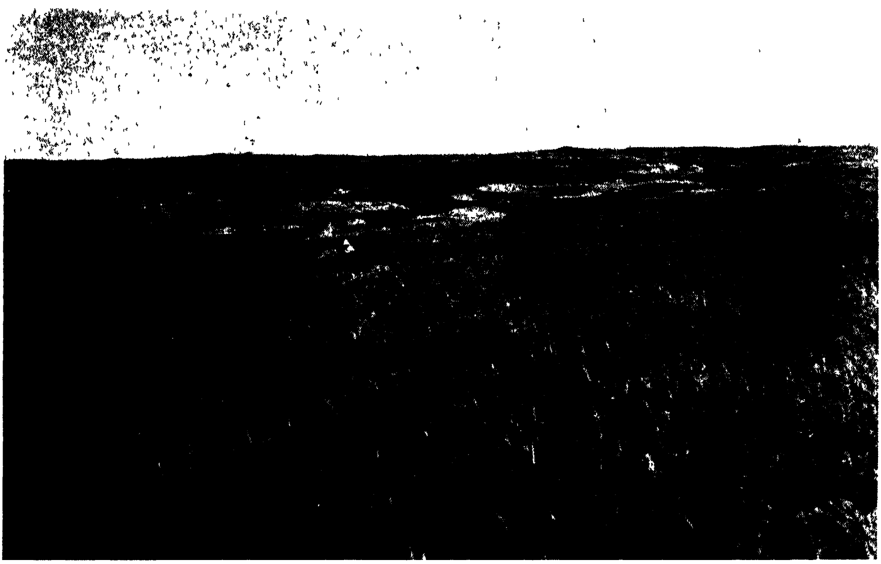

FIG. 3. Test area number 6, grama-needlegrass-sedge type on upland slope 26 miles southwest of Belfield. Dark stalks of *Artemisia dracunculoides* and white stalks of *Stipa comata* are conspicuous against the darker, shorter growth of *Bouteloua gracilis* and *Carex* spp. July 30, 1935.

TEST AREA NUMBER 6 (JULY 30, 1935, FIG. 3)

This area was located on a north-facing slope (5 to 10°), on the road to Ranger, 26 miles southwest of Belfield. The dominants were Bouteloua, Stipa, and Carex. The soil, Morton sandy loam (rolling phase) type, had developed apparently from sand of residual origin.

The abundance of *Bouteloua gracilis*, *Stipa comata*, Carex, and forbs, the fairly high total number of species on the area, the scarcity of *Agropyron smithii*, and the high percentage of bare ground (26 percent) were associated with a well-developed solum to a depth of 22 inches which is very sandy (70-82 percent); parent material composed chiefly of sand (83-87 percent); north-facing slope; freedom from excessive runoff and erosion; relatively low mois-

ture holding capacity (39-62 percent), low loss-on-ignition below 13 inches (1.7-2.8 percent), moderately high carbonate content (7.5-11 percent), and low concentration of soluble salts. The absence of Calamovilfa on this sandy soil was noteworthy.

Test Area Number 7 (August 6, 1935)

This area was located on a gentle south-facing slope, (less than 5°) 8.5 miles north of Grassy Butte (Sec. 31, T. 147, R. 199). The dominants were Bouteloua, Carex, Koeleria, Calamovilfa, and Stipa. The soil, Morton sandy loam type, appeared to have been developed from parent material residual from sandstone. Much land similar to this is under cultivation.

PROFILE DESCRIPTION

Morton sandy loam

Inches	
0-1.5	Dark brown to black, sandy loam. Pulverulent, readily friable. Roots numerous.
1.5- 3	Dark brown, sandy loam. Breaks into small clod-like fragments 1/4 to 1/2 inch in diameter, readily friable. Roots very numerous.
3-7.5	Dark brown, sandy loam. Prismatic structure, prisms 1 to 2 inches in diameter, very hard, breaking into irregular nut-sized pieces which are friable with difficulty to crumb. Roots numerous, follow cleavage planes mostly.
7.5-18	Brown, sandy loam. Poorly defined prismatic structure, becoming indistinct with depth. Prisms break into angular chunks 1/2 to 1 inch in diameter, more friable than the above horizon. Roots numerous, decreasing rapidly below 14 inches.
18-38	Brown sandy loam. Blocky structure, the soil falling out in angular pieces up to 1 inch in diameter and 2 inches long. Roots moderately numerous.
38-44	Tan colored, sandy loam. Irregular pieces falling readily into single grains, roots few.
44-60	Light tan sand, loose, roots scarce. No effervescence as deep as 60 inches.

This area was well developed prairie composed of 16 species of grasses and sedges and 37 species of forbs with an average of 16.9 species per meter square quadrat. The chief species were *Bouteloua gracilis, Carex stenophylla, C. pennsylvanica, Calamovilfa longifolia, Koeleria cristata, Stipa comata, Artemisia gnaphalodes*, and *Psoralea argophylla*. The presence of *Stipa spartea, Andropogon furcatus*, and *A. scoparius*, although in small numbers, indicated favorable conditions for prairie species. The sandy loam soil and gentle slope permitted ready penetration of precipitation. As indicated by the dark brown color and prismatic structure the solum was well developed, extending to a depth of 38 inches. Other distinctive aspects of the soil were high moisture holding capacity (62.8-64.8 percent) in the surface 7.5 inches for

a soil with such a high proportion of sand (58 percent), soil reaction mildly acid to depth of 27 inches, and the lack of excessive carbonates as tested by HCl to depth of 60 inches. The abundance of Calamovilfa and the scarcity of *Carex filifolia* in this area, and *vice versa* in area 6, may be due to lack of deep soil moisture in area 6, caused in part by the dominance of shallow-rooted grasses in number 6, while in this area deep moisture is probably present throughout most of the growing season. In area 7 the shallow-rooted plants were much less abundant than in area 6.

TEST AREA 8 (JUNE 20, 1934)

A long slope falling gently away from eroded buttes, 5 miles south of Sentinel Butte, was the site of this area (Sec. 9, T. 139, R. 104). The dominants were Bouteloua, Agropyron, and Stipa. The soil type was Patent clay.

The abundance of *Bouteloua gracilis* and *Agropyron smithii*, the scarcity of other grasses, and the small total number of species were associated with the high proportion of clay in the soil (averaging 46.5 percent to the working depth), gradual slope, shallow solum and carbonates and a pronounced carbonate layer at 34 to 44 inches. The severe drought of 1934 very likely decreased the number of species of forbs that might usually occur on this area.

TEST AREA 9

This area was located about 3 miles from area number 8 (Sec. 8, T. 139, R. 104). In topography, soil, and vegetation it was very similar to number 8. The dominants were Bouteloua, Agropyron, Stipa, and Carex. Only analyses of the vegetation were made in this area.

TEST AREA 10 (JUNE 17, 1935)

This area was located on a long, sweeping slope 11 miles northeast of Sentinel Butte (Sec. 35, T. 141, R. 103). The dominants were Agropyron, Bouteloua, and Carex. The soil originated, it appears, from outwash material eroded from a butte, of which only a remnant now remains. Much land similar to this is under cultivation and cropped chiefly to wheat.

DESCRIPTION OF A TYPICAL PROFILE IN A LONG GRADUAL SLOPE IN PATENT CLAY LOAM

Inches	
0 - 1	Dark brown, clay loam rich in organic matter. Fine crumby mulch, roots few to none.
1 - 4.5	Dark grayish-brown, clay loam. Slightly platy, effervescence moderately strong. Roots very numerous.
4.5-10.5	Light brown, clay. Soil breaks out in small nut-like fragments readily friable to small crumbs. Strong effervescence. Roots numerous.

10.5-27 Light grayish-brown clay. Blocky structure, soil falls out in hard angular fragments. Highly effervescent, roots fairly numerous to 22 inches, scarce below.

27 -50 Parent material. Light grayish-brown clay, compact and heavy, with small rock particles. Carbonates occur in streaks and blotches. Violently effervescent, roots infrequent, soil forms hard chunks when dry. Working depth of roots is 25 inches.

The abundance of *Agropyron smithii, Bouteloua gracilis*, and *Carex filifolia;* the scarcity or absence of other species of grasses; the low number of species on the area and per quadrat are associated with clay soil, shallow solum, carbonates within one inch of the surface and becoming pronounced at only 4.5 inches, high loss-on-ignition, alkaline reaction throughout and vegetation cover usually preventing excessive erosion. Soil and vegetation evidently have not reached maturity. Under cultivation this area would be subject to increased runoff and erosion.

TEST AREA 11 (JULY 5, 1935)

This test area on the Olstad Ranch, about 16 miles southeast of Sentinel Butte, was located on a long slope which stretched from the hills to a low terrace along an intermittent stream (Sec. 33, T. 139, R. 103). The dominants were Agropyron, Bouteloua, and Carex. The soil, Patent clay loam type, originated probably from material washed down from hills, now largely eroded away.

The abundance of *Bouteloua gracilis, Agropyron smithii*, and *Carex filifolia,* the scarcity or absence of other grasses, the fairly low total number (29) of species, were associated with clay loam to clay soil, shallow solum (14.5 inches), carbonates within 3.5 inches of the surface and a compact layer at 26 to 47 inches, alkaline reaction throughout, high calcium content, long gradual slope, and usually only moderate erosion. Soil and vegetation appear to be somewhat more developed than in area 10.

TEST AREA 12 (AUGUST 13, 1935, FIG. 4)

This area was located on the Olstad Ranch about 15 miles southeast of Sentinel Butte on a long gradual slope extending from a small upland plateau to a dry draw (Sec. 5, T. 138, R. 103). The dominants were Bouteloua, Agropyron, and Carex. The soil type was Patent clay loam.

The abundance of *Bouteloua gracilis, Agropyron smithii*, and *Carex filifolia*, the scarcity of other species of grasses, the fairly low total number (24) of species on the area and average number (6.8) per quadrat were associated with clay loam to clay except the surface 2 inches which have sandy loam texture, shallow solum (20 inches) alkaline reaction except surface 2 inches; carbonate content high beginning as shallow as 6 inches and extending as deep as dug (40 inches), long gradual slope and moderate ero-

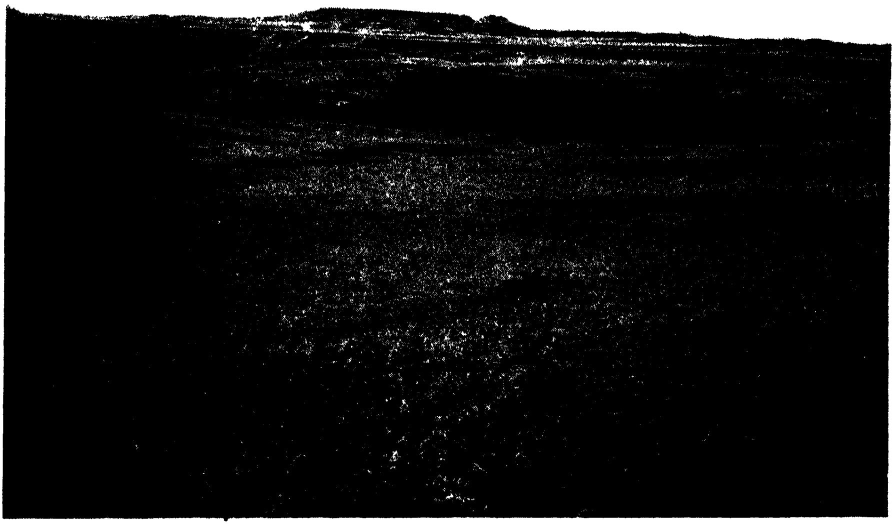

FIG. 4. Test area number 12, western wheatgrass-grama-sedge type, is on the long slope in the foreground, test areas 26, little bluestem type and 27, big bluestem type, on the hillside in center. Sentinel Butte in the distance. August 12, 1935.

sion. The sandy loam texture of the surface 2 inches may be a factor in the small increases in *Stipa comata* and *Carex filifolia* and the small decrease in *Agropyron smithii* in this test area as compared with areas 10 and 11 which did not have sandy texture in the surface layers. The vegetation and soil do not appear to have reached equilibrium.

TEST AREA 13 (JUNE 19, 1934)

This area was located on a long gradual slope 4 miles south of Medora (Sec. 11, T. 139, R. 102). The dominants were Bouteloua, Agropyron, and Carex. The soil, Patent clay loam type, appeared to have originated from local alluvium eroded away from buttes above, remnants of which are now present.

The dominance of *Bouteloua gracilis, Agropyron smithii,* and *Carex filifolia,* the low total number (12) of the species on the area, the low average number (3.7) of species per quadrat, and the absence or extreme scarcity of other species of grasses were associated with clay to clay loam texture, shallow solum (21 inches), alkaline reaction throughout, and carbonates beginning at the surface and becoming pronounced at 15 inches. Vegetation and soil appeared to be less developed in this area than in areas 10, 11, and

12, due probably to more recent origin and the slightly steeper slope which would favor greater runoff and erosion.

TEST AREA 14 (JULY 25, 1935, FIG. 5)

This area was located on the Olstad Ranch about 16 miles southeast of Sentinel Butte on a low terrace 8 to 12 feet above a stream in which stood

FIG. 5. Test area 14 on the terrace, with dominants, *Bouteloua gracilis*, *Agropyron smithii*, *Stipa comata*, and *Distichlis stricta* and scattered *Artemisia cana*. In the foreground shrubs are chiefly Symphoricarpos, Rosa, and Ribes; in draws Prunus, Amelanchier, Fraxinus. Fisher Run, 16 miles southeast of Sentinel Butte. July 24, 1935.

occasional pools of water (Sec. 33, T. 139, R. 103). The dominants were Bouteloua, Agropyron, Stipa, and Distichlis. The soil originated from materials washed down from surrounding higher land.

DESCRIPTION OF A TYPICAL PROFILE IN A LOW TERRACE IN HUFF SANDY LOAM

Inches	
0 - 1	Dark brown, sandy loam. Friable, brittle crust. Soil reacts mildly on the surface with HCl. Roots and rhizomes few.
1 - 3	Dark brown, sandy loam. Platiness slightly developed, soil digs out in irregular chunks readily friable to fine crumb, small pieces of scoria intermixed. Effervescence moderate, roots and rhizomes numerous.
3 - 7	Brown sandy loam, coarse angular structure, pieces readily friable. Moderate effervescence, roots numerous, rhizomes few.
7 - 8.5	Fine gravel, sand, and small pieces of scoria. Moderate effervescence, roots numerous, rhizomes scarce.

8.5-15.5 Brown, sandy loam. Soil digs out in angular nut-sized fragments, readily friable, occasional black flecks of lignite occur in the upper part of the horizon. Moderate effervescence, numerous roots, rhizomes scarce.

15.5-54 Parent material. Brown, sandy loam. White flecks in the soil mass and white accumulations along roots and old root channels, small pieces of lignite and scoria are intermixed. Strong effervescence, roots numerous to 25 inches, becoming scarce at 40 inches. Below 40 inches coarse gravel, large pieces of scoria and very heavy, greasy, blue clay. Working depth of roots 26 inches.

The unusual mixture of *Bouteloua gracilis, Agropyron smithii, Stipa comata*, and *Distichlis stricta*, the moderate number of species on the area (33) and per quadrat (9.2) were associated with dominantly sandy loam to depth of about 40 inches, heavy clay intermixed with gravel below 40 inches, very shallow solum (7 inches), usually favorable soil moisture, high sodium and total soluble salt concentrations below 15.5 inches, high carbonate content beginning at surface, and terrace topography. As the stream erodes a deeper channel, Distichlis and Agropyron may decrease on this area.

TEST AREA 15 (JUNE 20, 1935)

This area was located on a low terrace about 5 to 6 feet above a small, usually dry creek, along U. S. Highway No. 10, 8 miles east of Sentinel Butte (Sec. 22, T. 140, R. 103). The dominants were Agropyron and Distichlis. Soil developed on alluvial material.

DESCRIPTION OF TYPICAL PROFILE IN LOW TERRACE IN GORHAM CLAY LOAM

Inches

0 - 3 Grayish-brown loam, recently deposited, stratified, breaks into small angular fragments readily friable. Effervescence moderate, roots and rhizomes very numerous.

3 - 4 Dark brown to black clay loam, apparently containing much organic matter. Slightly developed platiness, soil breaks into small, friable, angular fragments. Mild effervescence, roots and rhizomes very numerous.

4 - 6 Dark brown, silt loam, apparently rich in organic matter. Soil digs out in small, friable, angular fragments. Moderate effervescence, roots very numerous.

6 -11.5 Dark brown, silt loam. Coarse blocky structure, soil digs out in large friable, irregularly angled chunks. Small white carbonate pockets which effervesce violently, soil mass streaked with white showing only moderate effervescence. Roots numerous.

11.5-12 Dark brown to black, silt loam, apparently containing considerable organic matter. Former surface horizon having slight indications of a former platiness. Effervescence moderate, roots numerous, rhizomes few.

12 -20.5 Grayish-brown silt loam. Coarse blocky structure, soil digs out in large chunks which crumble readily to small angular fragments.

	Effervescence moderate, roots numerous, rhizomes found down to 18 inches.
20.5-21	Another dark brown horizon, apparently rich in organic matter, roots numerous. This horizon is very similar to the 11.5 to 12 inch layer.
21 -60	Grayish-brown loam. Layer from 22 to 28 inches is hard, apparently contains much salt. Below 51 inches scoria and lignite particles intermixed, effervescence moderate. Working depth of roots 22 inches. Dead roots indicate that the working depth in previous years has been about 29 inches. Old root channels marked by incrustations of white salts.

The abundance of *Agropyron smithii* and *Distichlis stricta*, the scarcity of grasses as *Bouteloua gracilis* and *Stipa comata*, the moderate number of forbs (25) and of total species (36) on the area, the fairly low number (7.9) of species per quadrat were associated with soil texture of chiefly silt loam, high content of carbonates beginning at surface, fairly high concentration of soluble salts at surface and becoming greater below 6 inches, very high to medium high concentration of calcium, high moisture holding capacity especially in the 3 to 4-inch layer, alkaline reaction throughout, and usually ample moisture for plant growth fairly close to surface. The higher amounts of clay, salt, and moisture in the surface foot of soil in this area as compared to number 14, may account for the small amount of *Bouteloua gracilis* and *Stipa comata* and abundance of *Agropyron smithii*. Poor aeration below one foot may also be a factor.

TEST AREA 16 (JUNE 21, 1935)

This area was located on a flat bordering a shallow water course along U. S. Highway No. 10, 8 miles east of Sentinel Butte (Sec. 22, T. 140, R. 103). It was 4 or 5 feet lower than area 15. The dominants were Distichlis and Puccinellia. The soil, Gorham clay loam type, originated from water deposited material.

The abundance of *Distichlis stricta*, *Puccinellia nuttalliana*, and the presence of *Hordeum jubatum*, the scarcity of *Agropyron smithii*, the absence of other grasses as *Bouteloua gracilis* and *Stipa comata*, the fairly low number of total species on the area (24) and per quadrat (6.6) and the shallow working depth of the roots (now 18, formerly 26 inches) were associated with the loam to silty clay texture, high colloidal content, the unusually high concentration of soluble salts beginning at the surface and extending to 54 inches (1,587 to 11,100 p.p.m.), the high carbonate content throughout the profile (17.6 to 21.5 percent), the high calcium content, and, usually, the large amount of soil moisture close to the surface. Lack of aeration may also be an important factor.

TEST AREA 17 (JUNE 25, 1935, FIG. 6)

This area was located on a low terrace 8 to 10 feet above Garner Creek on the Olstad Ranch about 16 miles southeast of Sentinel Butte (Sec. 34, T. 139, R. 103). The dominants were Agropyron, Distichlis, and Bouteloua. The soil, Gorham sandy loam type, originated from material deposited by flood waters as in the summers of 1935 and 1929.

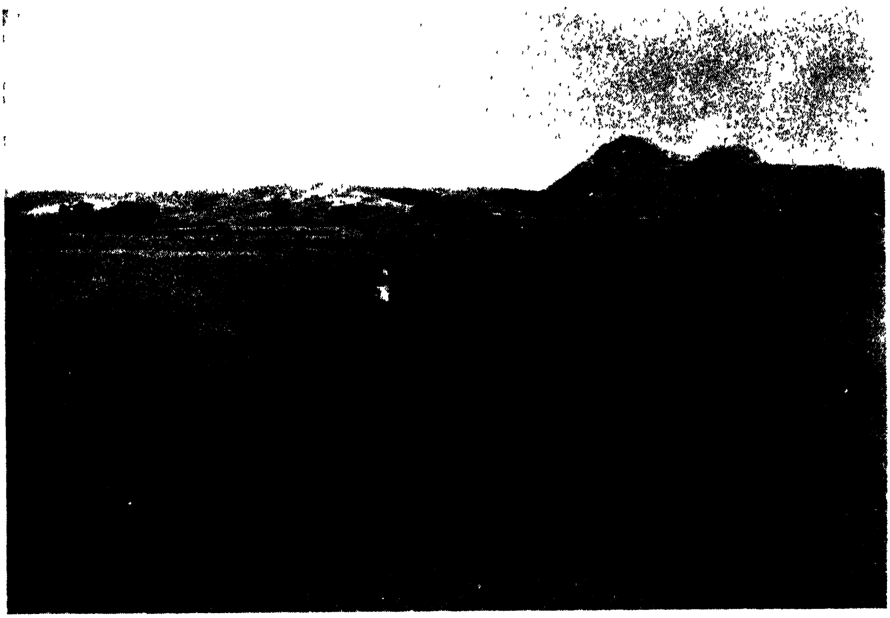

FIG. 6. Test area 17, saltgrass-western-wheatgrass type, on a terrace along Garner Creek, 16 miles southeast of Sentinel Butte. Trees are chiefly *Fraxinus pennsylvanica*, shrubs along creek are mostly *Symphoricarpos occidentalis*, *Rosa woodsii*, and *Ribes* spp. July 10, 1935.

The abundance of *Agropyron smithii*, *Distichlis stricta*, and *Bouteloua gracilis*, the presence of *Stipa viridula* and *Artemisia cana*, the scarcity of *Stipa comata*, the low total number (28) of species on the area and the low average number of species per quadrat, and the scarcity of forbs were associated with chiefly loam texture, high concentration of soluble salts, especially sodium, below 20 inches, large amounts of carbonates even in the surface soil, alkaline reaction throughout, and soil moisture usually plentiful near the surface and excessive below 2 or 3 feet. The smaller amount of *Stipa comata* on this area as compared with area 14, which is somewhat similar, may be due to excessive soil moisture and higher clay content.

TEST AREA 18 (JUNE 26, 1935)

Area 18 was located on a nearly level flat about 12 feet above Garner Creek on the Olstad Ranch, 16 miles southeast of Sentinel Butte (Sec. 5,

T. 138, R. 103). Although dominantly a sagebrush *(Artemisia cana)* type, it was well grassed. The dominants in addition to sagebrush were Bouteloua, Agropyron, and Stipa. The height of the sagebrush made it impracticable to use the point system. The material from which the soil developed was largely flood deposited.

DESCRIPTION OF TYPICAL PROFILE IN SAGEBRUSH FLAT IN CHERRY CLAY

Inches	
0- 2	Dark brown clay. Slightly developed platiness, readily friable, becoming light and puffy on being pulverized. Mild effervescence on surface, roots few, rhizomes frequent.
2- 7	Dark brown clay, definite platy structure, friable. Moderate effervescence, roots numerous, rhizomes frequent.
7-11	Brown clay, prismatic structure, breaks into small nut-like chunks 1/2 to 1 inch in diameter, friable. Effervescence moderate, increasing with depth, roots very numerous.
11-18	Light brown clay, coarse prismatic structure, falls out in large friable chunks up to 2 inches in diameter. Effervescence moderate, somewhat stronger than in above horizon, roots numerous.
18-27	Light brown clay, blocky structure, digs out in irregular chunks up to 4 inches long and 2 inches in diameter. A hard, compact layer. Effervescence moderate to violent, streaks of carbonate appear in the lower part of the horizon. Roots fairly numerous, particularly of sage, other roots follow sage roots.
27-61	Parent material. Light brown clay, stratified, very hard and dry, marked throughout with white streakings. Strong effervescence, grass roots few, sage roots continue to below 60 inches. Working depth of roots 31 inches.

The abundance of *Artemisia cana, Bouteloua gracilis, Agropyron smithii,* and *Stipa viridula,* the large number (50) of total species on the area, and the low frequency-abundance of forbs were associated with soil mainly clay in texture, soluble salts not excessive, carbonates fairly high below 11 inches, high loss-on-ignition of surface 11 inches, alkaline reaction throughout, solum 18 inches deep, nearly level topography, and subsoil moisture available throughout season, at least below 5 feet. The absence of Distichlis may be due to lack of excessive soluble salts and moisture in the surface 2 to 3 feet.

TEST AREA 19 (JUNE 19, 1935, FIG. 7)

A narrow valley, subject to frequent flooding following rains, 4 miles north of Medora and about a quarter of a mile from the Little Missouri River was selected for this area (Sec. 29, T. 141, R. 101). The vegetation was predominantly *Artemisia cana.* Because of the height and spread of the sagebrush it was impracticable to use the point method. The parent material had mostly been deposited from flood waters.

FIG. 7. Test area 19, sagebrush type, about 4 miles north of Medora. June 19, 1935.

DESCRIPTION OF A TYPICAL PROFILE OF SAGEBRUSH FLAT IN MEDORA SILT LOAM

Inches	
0 - 0.5	Light gray, silt loam, recently deposited, stratified, forming dry powdery surface crust which blows readily. Mild effervescence, no roots.
0.5-12.5	Grayish-brown, silt loam, stratified, occasional scoria pockets. Moderate effervescence, roots numerous.
12.5-48.5	Gray, uniform deposit of silty clay loam, laminated, occasional small pockets of lignite particles. Moderate effervescence, roots numerous.
48.5-53	Grayish, sandy loam containing numerous small particles of scoria. Moderately strong effervescence, roots numerous.
53 -64	Very fine sand and silt, laminated, occasional streaks of fine coal particles, moderate effervescence. Working depth of roots 52 inches. Roots fairly numerous again between 60 and 65 inches.

The abundance of *Artemisia cana* and *Agropyron smithii*, the presence of *Stipa viridula* and *Stipa comata*, the scarcity of forbs and other species of grasses, the moderate number (31) of total species on the area, and the low average number per quadrat were associated with recently deposited silt loam to 4 feet in depth, slightly alkaline reaction throughout, somewhat greater concentration of soluble salts than in the similar area number 18, fairly high carbonate content beginning at the surface, small amount of so-

dium below 4 feet, and moisture usually available below 4 or 5 feet. As in area 18 the lack of excessive salts and moisture within the surface 2 or 3 feet may account for the absence of Distichlis.

TEST AREA 20 (JUNE 22, 1934)

This area was located on a large flat along the Little Missouri River just north of the mouth of Garner Creek (Sec. 28, T. 139, R. 102). The dominance of sagebrush made it impossible to use the point system. Agropyron. Bouteloua, and *Stipa viridula* were dominants between the sagebrush. The soil type was Medora clay loam. Parent material has been recently deposited, chiefly by flood waters.

The abundance of *Artemisia cana, Agropyron smithii, Bouteloua gracilis,* and *Stipa viridula*, the moderate abundance of forbs, the small number (23) of total species, and the low average number (5.1) of species per quadrat were associated with recently deposited clay or silty clay to depth of 25.5 inches underlaid by fine sandy loam, alkaline reaction throughout, carbonates beginning at the surface and maximum concentration at 25.5 to 29.5 inches; and subsoil moisture available throughout season only below 3.5 feet or more.

TEST AREA 21 (JULY 15, 1935)

A sandy, upland ridge on the Olstad Ranch about 16 miles southeast of Sentinel Butte was selected (Sec. 4, T. 138, R. 103). The chief dominant was Calamovilfa.

DESCRIPTION OF TYPICAL PROFILE IN BAINVILLE FINE SAND

Inches	
0-6	Grayish-brown, fine sand, single grain structure, shows somewhat the influence of organic matter. Mild effervescence, rhizomes numerous in upper 3 inches, roots abundant below this.
6-64	Loose, undifferentiated, light grayish-brown, sandy loam with occasional pieces of scoria and friable sandstone intermixed. Moderate effervescence, roots numerous.
64-67	Light grayish-brown fine sand. Horizon of carbonate accumulation, strong effervescence, small granules of carbonate material effervesce violently. Roots numerous.
67-74	Light grayish-brown fine sand, loose, moderate effervescence. Working depth of roots at 70 inches, maximum depth below 10 feet.

The dominance and abundance of *Calamovilfa longifolia;* the abundance of *Carex filifolia, Stipa comata,* and *Bouteloua gracilis,* the presence of *Koeleria cristata, Andropogon scoparius, Andropogon hallii, Meriolix serrulata, Yucca glauca,* and other forbs, the scarcity of *Agropyron smithii,* the fairly large total number (42) of total species, and fairly large average number (12.6) per quadrat were associataed with soil texture of fine sand to

sandy loam, low soil colloid content, moderate moisture holding capacity, very low loss-on-ignition, alkaline reaction throughout, fairly high carbonate content throughout, low amount of total soluble salts, low calcium content, and usually available soil moisture throughout the season at some depth in the soil.

TEST AREA 22 (AUGUST 1, 1935, FIG. 8)

This area was selected on an 8° south-facing, upland slope, 25 miles southwest of Belfield along the Ranger road. Dominants were Calamovilfa and Carex. The parent material appeared to be residual in origin. The soil type was Bainville sandy loam (rolling phase).

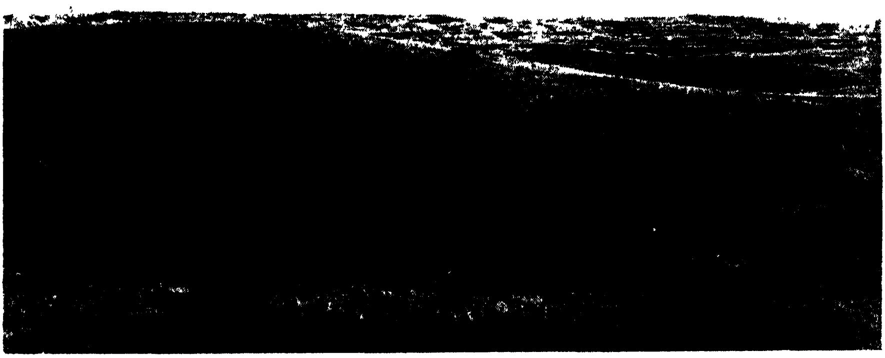

FIG. 8 Test area 22, sandgrass type, on a south facing slope, 25 miles southwest of Belfield. August 1, 1935.

The abundance of *Calamovilfa longifolia* and *Carex pennsylvanica,* the fairly high frequency-abundance of *Stipa comata* and *Carex filifolia*, the presence of *Bouteloua gracilis, Koeleria cristata*, and *Andropogon scoparius,* the scarcity of *Agropyron smithii*, the fairly high total number (40) of species, and the moderate average number (9.9) of species per quadrat were associated with a highly uniform sandy loam texture, low colloidal content, moderate moisture holding capacity, small amount of soluble salts and carbonates, low loss-on-ignition, acid reaction throughout, medium amount of Ca throughout, very high concentration of K in the surface foot, fairly well developed solum to 19 inches, moderate slope well covered with plant débris so that runoff and erosion were negligible. Soil and vegetation on this area showed considerably more development than in area 21. It seems that Calamovilfa should be less abundant and *Stipa comata* more abundant on area 22 than on area 21 but the opposite was true. The higher carbonate

content and alkaline reaction throughout the profile in area 21 may be important factors. Grazing in the past, an unknown factor, may also be important in determining such differences. This emphasizes that long time records of all factors are essential in basic investigations.

Test Area 23 (July 31, 1935)

This area was located on an upland, south-facing slope (8 to 10°), 26 miles southwest of Belfield, along the Ranger road. The dominants were Calamovilfa, Carex, and Stipa. It was selected because it appeared to have less of the first and more of the last than area 22. The soil material appeared to be residual in origin. The soil type was Bainville (rolling phase).

The abundance of *Calamovilfa longifolia*, Carex, and *Stipa comata*, the presence of *Bouteloua gracilis* and *Koeleria cristata*, the absence of *Agropyron smithii*, the fairly high total number (42) of species on the area, the moderate average number (10.7) of species per quadrat were associated with sandy loam texture, fairly well developed solum to depth of 17.5 inches, moderately low amount of colloidal matter, fairly high moisture holding capacity, low loss-on-ignition, acid reaction to 42 inches, low amount of soluble salts and calcium, and gentle slope permitting ready penetration of water. Comparison of this area with number 6, which was located on the north facing slope of the same hill, shows that number 6 had more *Bouteloua gracilis* and *Stipa comata* and no *Calamovilfa longifolia*. The only important differences in soil conditions were that area 6 had a deeper solum (29.5 in.), higher sand content, and greater amount of carbonates especially below 22 inches. The direction of the slope may have been of major importance since the surface soil would dry more rapidly on the south-facing slope (area 23) than on the north-facing slope (area 6).

Test Area 24 (June 25, 1934)

This area was located on a gentle upland slope (5 degrees or less), facing south to southeast, 9 miles southeast of Sentinel Butte (Sec. 7, T. 139, R. 103). Dominants were Calamovilfa and Carex. The soil type was Morton fine sandy loam.

The abundance of *Calamovilfa longifolia*, and *Carex* spp., the presence in moderate numbers of *Bouteloua gracilis*, *Stipa comata*, and *Koeleria cristata*, the presence in small numbers of *Andropogon scoparius*, *Aristida longiseta*, and *Panicum wilcoxianum*, the scarcity of *Agropyron smithii*, the moderate total number (35) of species on the area, and the moderate average number (10.2) of species per quadrat were associated with sandy loam texture, fairly low colloidal content of soil, acid reaction to 39 inches, solum moderately developed extending to 23 inches in depth, no effervescence to depth of 72 inches, and moderate slope permitting ready penetration of water.

TEST AREA 25 (JULY 20, 1935)

This area was located on the lower part of a 20 to 25° slope on the Olstad Ranch about 16 miles southeast of Sentinel Butte (Sec. 33, T. 139, R. 103). *Andropogon scoparius* was dominant.

DESCRIPTION OF TYPICAL PROFILE IN LITTLE BLUESTEM TYPE IN BAINVILLE FINE SANDY LOAM (STEEP PHASE)

Inches	
0-1.5	Dark brown sandy loam, fine crumb structure, moderate effervescence, roots few, rhizomes few.
1.5- 4	Dark Brown sandy loam. Soil forms small angular fragments which are friable to fine crumbs. Effervescence moderate but somewhat stronger than in horizon above, roots numerous.
4- 7	Brown silty clay loam, fragmentary structure. Angular fragments range from 1/4 to 3/4 of an inch in diameter, readily friable. Effervescence moderate, roots numerous.
7- 12	Dark gray silty clay, fragmentary structure. Angular fragments friable to fine light powder, strongly effervescent, roots numerous.
12- 53	Parent material. Gray silt loam, definitely stratified, streaked and mottled with iron stains. Strongly effervescent, roots numerous. Below 20 inches were alternate layers of fine sand and clay also stained and mottled. No definite zone of carbonate accumulation. Working depth of roots 26 inches. Roots very few at 53 inches.

The abundance of *Andropogon scoparius*, and the presence of numerous other species of grasses and forbs making a total of 52 on the area and an average of 12.8 per quadrat were associated with a fairly steep slope (20° to 25°), shallow solum (7 inches), texture of surface 4 inches sandy loam, underlaid by horizons of silty clay loam, silty clay and silt loam, high moisture holding capacity, and usually ample moisture for plant growth throughout the season at least below one foot, slightly alkaline reaction throughout, very high amounts of carbonates (21 to 30 percent) in all horizons except surface 1.5 inches, low amounts of soluble salts, and calcium content medium to high. Because of the fairly steep slope this area was subject to considerable runoff and erosion but the dense cover of vegetation furnished full protection.

TEST AREA 26 (AUGUST 12, 1935, FIG. 4)

This area was located on a 15 to 20° northeast facing slope, about 18 miles southeast of Sentinel Butte (Sec. 7, T. 138, R. 103). *Andropogon scoparius* was the dominant. The point system was not used because of the height of the vegetation. The soil type was Bainville loam (strongly rolling phase).

The abundance of *Andropogon scoparius,* and the presence in small numbers of many other species of grasses, sedges, and forbs, totaling 46 for the area and averaging 10.8 per quadrat, were associated with a fairly steep slope (15 to 20°), solum 18 inches deep, soil texture loam to silty loam, high

moisture holding capacity and usually adequate moisture below 2 feet for plant growth throughout the season; high carbonate content in all horizons, alkaline reaction throughout, and low loss-on-ignition and soluble salt content. The vegetation cover was dense so the slope was protected from excessive runoff and erosion.

TEST AREA 27 (AUGUST 15, 1935, FIG. 4)

This area was located on the lower part of a steep slope about 18 miles southeast of Sentinel Butte (Sec. 7, T. 138, R. 103). The chief dominant was big bluestem *(Andropogon furcatus)*. The soil type was Bainville fine sandy loam (rolling phase, small draw).

The dominance of *Andropogon furcatus,* the presence of *Andropogon scoparius, Bouteloua curtipendula,* Carex, and *Elymus glaucus,* the large total number (55) of species on the area and large average number (13.0) per quadrat, and the very low percentage of bare soil (2) were associated with a well developed, deep solum (36 inches), soil texture almost entirely loam becoming heavier with depth, high content of colloidal matter, high moisture holding capacity and usually available moisture for plant growth throughout the season, low content of soluble salts, calcium abundant below 3 feet, rather high loss-on-ignition, moderate carbonate content in upper 3 feet but high below, very slightly acid reaction to 20 inches, and topographic location on lower part of slope which provided additional moisture by runoff and, possibly, seepage from hill above.

TEST AREA 28 (AUGUST 2, 1935)

The steep slopes of the banks and side ravines of a narrow valley 8 miles south of Fryburg were selected as the site of this area. The chief dominant was big bluestem *(Andropogon furcatus)*. Moisture conditions appeared to be especially favorable due to seepage. Because of the height of the vegetation the point system was not used.

DESCRIPTION OF TYPICAL PROFILE IN BIG BLUESTEM TYPE IN BAINVILLE LOAM (STEEP PHASE)

Inches	
0 - 0.25	Loose, dry, dead leaves on the surface.
0.25- 1.5	Dark-brown mixture of fibrous material, roots, leaves, and old stems, mixed with mineral matter. Very light, soft and loose. Rhizomes numerous at bottom of this layer.
1.5 - 4	Dark, reddish-brown loam, small scoria particles intermixed. Breaks out into irregular pieces 1/4 to 1/2 of an inch in diameter, friable to small crumbs. Roots very numerous, rhizomes few.
4 - 9	Dark brown, clay loam. Fragmentary structure, small angular pieces hard and friable only with difficulty to fine crumbs, numerous scoria particles from 1/4 to 3/4 of an inch in length. Roots very numerous.

9 -17.5	Grayish-brown, clay to clay loam. Fragmentary structure, angular fragments range in size from 1/4 to 3/4 of an inch in diameter, friable with some difficulty to crumbs. Scoria particles numerous, occurring in horizontal layers. Roots very numerous.
17.5 -25	Grayish-brown loam, almost structureless. Scattered scoria particles are imbedded in the soil mass which is stained with occasional iron streakings. Moderate effervescence, fine roots very numerous.
25 -45	Parent material. Grayish-brown loam, grading into laminated deposits of play and sand, impervious blue clay layer 3 inches thick at 39 inches. Roots very numerous, decreasing abruptly at 32 inches, moderate effervescence. Working depth of roots 33.5 inches.

The dominance of *Andropogon furcatus*, the abundance of *Andropogon scoparius* and *Carex pennsylvanica*, the presence of prairie needle grass (*Stipa spartea*) and numerous other species of grasses and forbs making the high total number of 63 species on the area and high average number of 17.1 per quadrat were associated with loam to clay loam texture of soil, very high moisture-holding capacity and available moisture for plant growth during most of growing season, low loss-on-ignition except in surface 4 inches where it was high, acid reaction to 17.5 inches, low content of carbonates, soluble salts, and calcium, and topographic location at base of slopes where extra moisture would be received by runoff and seepage from slopes above.

TEST AREA 29 (JUNE 26, 1934)

This area was located on the lower part of a steep slope about 4 miles south of Sentinel Butte (Sec. 9, T. 139, R. 104). The crest of the hill was gravelly. The chief dominant was *Andropogon furcatus*. Soil originated, probably, from local alluvium from the slope above. The soil type was Bainville loam (steep phase).

The dominance of *Andropogon furcatus*, the moderate abundance of *Andropogon scoparius* and *Carex stenophylla*, the presence of species such as *Bouteloua curtipendula*, *Elymus glaucus*, *Aster laevis*, and *Campanula rotundifolia*, the fairly high total number of species on the area (41) and per quadrat (12.2) were associated with steep slope probably receiving additional moisture by runoff and seepage from above, sandy loam surface soil underlaid by loam, clay loam, and clay (63 percent clay content below 22 inches), alkaline reaction, extremely high colloidal content beginning at 22 inches, and dark brown solum.

TEST AREA 30 (AUGUST 5, 1935, FIG. 9)

This area was located on the lower parts of a gentle north-facing slope, near the edge of the breaks of the Little Missouri River valley about 16 miles

FIG. 9. Clumps of *Sporobolus heterolepis* forming dense stand with *Andropogon furcatus, Stipa spartea, Calamovilfa longifolia, Carex* spp., and many others, in test area 30, about 16 miles north of Kildeer. August 5, 1935.

north of Kildeer. This area was the best developed prairie type studied. It was characterized by the dominance of Sporobolus, Andropogon, Carex, Stipa, and Calamovilfa.

PROFILE DESCRIPTION OF DROPSEED-BIG BLUESTEM TYPE IN MORTON FINE SANDY LOAM (DARK PHASE)

Inches	
0 - 0.25	Decaying leaves and stems.
0.25- 1	Black sandy loam, crumb structure. Light in weight, containing much decaying vegetation, roots fairly numerous.
1 - 4	Dark brown to black, sandy loam. Light in weight, granular, readily friable, roots very numerous.
4 -11	Dark brown to black, sandy loam. Coarse, soft crumb structure, readily friable. Roots very numerous.
11 -18	Dark brown sandy loam, digs out in angular, nut-like pieces that are soft and friable. Roots very numerous.
18 -28	Brown sandy loam, blocky structure. Soil digs out in irregular chunks up to 2 inches thick, easily friable. Roots very numerous.
28 -33	Light brown sandy loam, almost structureless. Soil digs out in coarse, soft, irregular pieces that crumble easily to single grains. Roots numerous. Transitional to parent material.
33 -54	Parent material. Light brown, loose sand, strongly effervescent. Roots fairly numerous to 38 inches, almost none at 40 inches. Working depth 38 inches.

The abundance of *Sporobolus heterolepis, Carex pennsylvanica, Andropogon furcatus, Calamovilfa longifolia,* and *Stipa spartea;* the presence of certain species as *Koeleria cristata, Stipa viridula, Juncus balticus, Anemone cylindrica, Pulsatilla hirsutissima, Monarda fistulosa, Castilleja sessiliflora,* and *Lilium umbellatum;* the large number of species found in the area (86) and per quadrat (20.3); working depth of 38 inches; and the luxuriance of the vegetation (see Fig. 9) were associated with sandy loam soil on the lower portions of northerly slopes where the soil moisture received directly from precipitation would be increased by melting of snowdrifts, runoff from slopes, and, possibly, seepage. The solum was unusually dark in color for western North Dakota, extending to depth of 28 inches. The surface soil had high moisture holding capacity, loss-on-ignition, and Ca and K contents. The carbonate content was low as deep as the parent material below 33 inches. The total soluble salts were low, colloidal content moderate, and the soil was slightly acid to depth of 28 inches.

TEST AREA 31 (AUGUST 12, 1935)

This area was located about 18 miles southeast of Sentinel Butte (Sec. 8, T. 138, R. 103). It was located on a northerly slope of about 10 to 15°. The soil material originated, apparently, from hills above, now mostly eroded away. The soil type was Bainville loam (strongly rolling phase). Because of grazing on this area the vegetation was analyzed by observation only. The dominant species was *Andropogon scoparius.* In places *Carex filifolia* was abundant, in others infrequent. Other species were usually scarce. The most common were *Koeleria cristata, Calamovilfa longifolia, Agropyron smithii, Bouteloua gracilis,* and *Echinacea angustifolia.*

The dominance of *Andropogon scoparius,* the presence of species usually found in this type, and working depth 42 inches were associated with fairly shallow, poorly developed solum (17 inches deep), loam to clay loam soil with moderately high colloidal content, high percentage of carbonates and calcium beginning at the surface, soil mildly alkaline at the surface and increasing to pH 8.21 at 17 inches, low loss-on-ignition and total soluble salts.

TEST AREA 32 (JULY 27, 1935)

This area was located on the lower parts of steep slopes on the south side of a plateau on the Olstad Ranch about 15 miles southeast of Sentinel Butte (Sec. 5, T. 138, R. 103). The soil originated from material washed down from higher slopes. The soil type was Morton loam (rolling phase). Because of grazing the vegetation was studied only by observation. *Andropogon furcatus* was the dominant and *Bouteloua curtipendula* was fairly abundant. Some of the other species were *Agropyron smithii, Panicum virgatum, Stipa viridula, Koeleria cristata, Andropogon scoparius, Artemisia gnaphalodes, Achillea lanulosa,* and *Symphoricarpos occidentalis.*

The dominance of *Andropogon furcatus,* the presence of other characteristic species listed above, and the high density of the vegetation were associated with the physiographic location (base of steep slopes) where moisture is received by runoff from above, from melting snowdrifts and probably by seepage; soil texture chiefly sandy loam; dark colored, well developed solum to depth of at least 25.5 inches; high water-holding capacity, high loss-on-ignition in 1 to 3-inch layer, low carbonate content to depth of 40 inches, slightly acid reaction to depth of 32 inches, and small quantities of soluble salts throughout.

Test Area 33 (August 8, 1935)

This area was located on lower slopes and in bottoms of small draws or swales in a valley, not subject to overflow, about 8 miles west of Dickinson. The frequency-abundance and point methods were not used because the area was grazed. *Buchloe dactyloides* was dominant and *Agropyron smithii* was abundant. Other species occurring infrequently were *Bouteloua gracilis. Stipa viridula, Poa buckleyana,* and *Carex stenophylla.*

DESCRIPTION OF PROFILE IN BUFFALO GRASS TYPE IN GRAIL SILTY CLAY LOAM

Inches	
0 - 1	Grayish-brown clay. Soft, friable crumb structure, somewhat platy. Roots numerous, rhizomes frequent.
1 - 7	Dark-brown to black clay. Poorly defined prismatic structure, vertically elongated chunks break into small, hard, angular fragments about 1/4 to 3/4 inch thick. Roots very numerous.
7 -13.5	Brown clay. Poorly defined prismatic structure, prisms break into hard angular fragments. Effervescence moderate, roots numerous.
13.5-25	Light-brown clay. Angular fragmentary structure, friable only with difficulty. Violent effervescence, white flecks and streaks numerous. Black layer, 1 inch thick, at bottom of this horizon did not effervesce. Roots numerous.
25 -32	Light brown, sandy clay loam, almost structureless. Digs out in irregular, hard, angular pieces. Effervescence occurs only in occasional pockets, white streakings few, roots frequent.
32 -42	Brown, compact clay with occasional white streaks. Effervescence moderate to strong, roots infrequent. Working depth 33 inches.

The dominance of Buchloe, the abundance of *Agropyron smithii,* and the presence of other species as *Bouteloua gracilis* and Poa, were associated with soil containing a high proportion of clay and much colloidal matter, high soluble salt content especially below 32 inches, slightly alkaline soil reaction, low loss-on-ignition, fairly low carbonate content, and unusually strong effervescence in the 13.5 to 25-inch layer which was marked by numerous white streaks and flecks.

Test Area 34 (August 7, 1935, See Fig. 10)

This area was located on a fairly high level area between hills about 10 miles northwest of Kildeer along N. D. Highway No. 22. Examination of

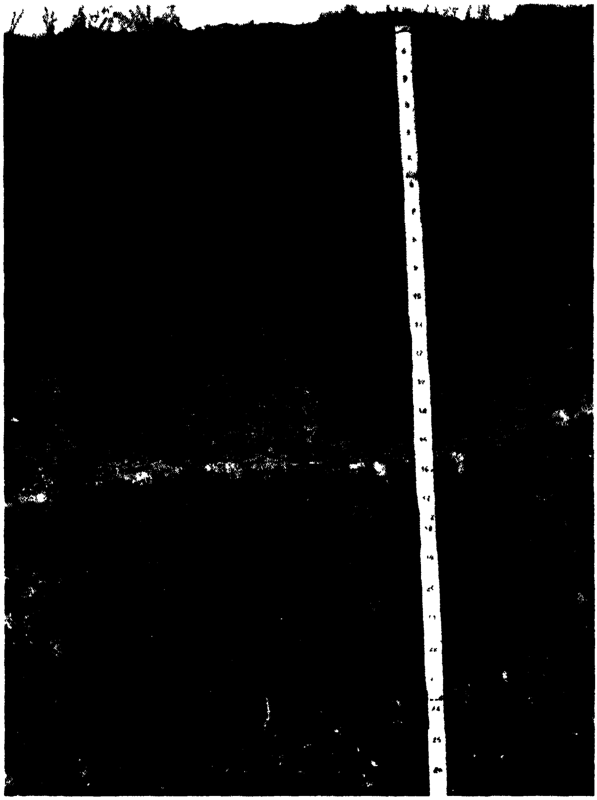

FIG. 10. View of soil profile, similar to that in test area 34, showing solodized solonetz structure on Morton Loam, solonized phase, near Grassy Butte "The caps of the columns are slightly exposed in the picture, that is, there is a little shelf at that point The soil above the column shows some relicts of an old prismatic structure but when removed they are very friable. In places this soil shows a definite platy structure. The upper 4 or 5 inches of the columns is very dark brown clay, very hard when dry, and breaks into angular small nut-size pieces that are nearly cubical. The picture shows the mottling of white in the lime zone beginning at about 23 inches. The cover on the uneroded soil was largely grama grass" Photograph and description by Charles E. Kellogg, Chief, U. S. Soil Survey.

the vegetation showed that *Bouteloua gracilis* was the chief dominant. *Poa buckleyana* occurred frequently. *Agropyron smithii, Stipa viridula,* and *Stipa comata* were scarce. The soil type was Patent silty clay loam.

The dominance of *Bouteloua gracilis* in mixture with *Poa buckleyana* and a few other grasses was associated with soil containing a high percentage of clay (24.5 to 36.7 percent); high colloid and calcium contents, fairly high concentration of soluble salts below 30.5 inches, no effervescence above 23 inches but strong below 37.5 inches, well developed solum to depth of about 23 inches, slightly acid reaction to 23 inches, and low loss-on-ignition.

TEST AREA 35 (AUGUST 7, 1935, FIG. 11)

This area was located on a flat area between low hills about 3 miles northwest of Kildeer along N. D. Highway No. 22. The chief dominants were *Distichlis spicata* and *Puccinellia nuttalliana. Agropyron smithii* was also

FIG. 11. *Puccinellia airoides* in mixture with *Distichlis spicata* and some *Agropyron smithii*, as in area 35, saltgrass-alkali meadowgrass type. About 16 miles north of Kildeer. August 5, 1935.

abundant. Other characteristic species were *Plantago elongata, Atriplex argentea, Dondia depressa,* and *Opuntia fragilis.*

DESCRIPTION OF PROFILE IN SALTGRASS TYPE IN PATENT CLAY LOAM (STRONGLY SOLONIZED PHASE)

Inches	
0 - 1.5	Light gray, fine sandy loam. Somewhat platy structure, vesicular, brittle, pulverizes easily to fine crumbs. Roots few.
1.5- 4	Grayish brown loam. Columnar structure, columns very hard, rounded caps fairly well developed. Roots very numerous, rhizomes numerous.
4 - 8	Grayish-brown clay. Prismatic structure, prisms about 2 inches in diameter, very hard. Effervescence moderate, roots numerous, rhizomes frequent.
8 -14	Grayish-brown silt loam. Prismatic structure less well developed than in layer above. Effervescence moderate, roots frequent.
14 -19	Brown clay, poorly defined prismatic structure, effervescence moderate, roots frequent.
19 -37	Brown clay, with some white mottlings. Massive, dry pieces very hard. Effervescence moderate, roots infrequent.
37 -42	Parent material. Yellowish brown clay, effervescence moderate, roots infrequent to scarce. Working depth of roots 26 inches.

The dominance and abundance of Distichlis, Puccinellia, and *Agropyron smithii*, and the presence of Dondia, Atriplex, Opuntia, and Plantago were associated with unusually high concentration of soluble salts below 1.5 inches, reaching 13,900 p.p.m. in the 8 to 14-inch layer, unusually high concentration of sodium throughout the profile, potassium content high to depth of 19 inches, high percentage of clay and colloids in most of the horizons, fairly high alkaline reaction between 4 and 19 inches, low loss-on-ignition, moderately large amount of carbonates below 8 inches, and shallow solum of about 14 inches.

TEST AREA 36 (AUGUST 7, 1935)

This area was located on a gently sloping upland about 5 miles northwest of Kildeer along N. D. Highway No. 22. Dominants were *Bouteloua gracilis* and *Stipa comata*. *Carex stenophylla* and *C. pennsylvanica* were difficult to distinguish and together rated as abundant. Other important species were *Agropyron smithii*, *Calamagrostis montanensis*, *Carex filifolia*, *Malvastrum coccineum*, and *Collomia linearis*. The soil type was Morton sandy loam.

The dominance of Bouteloua, Stipa, and Carex, the presence of numerous other species, and the deep working level of 51 inches were associated with chiefly sandy loam texture, moderately low colloidal content, low loss-on-ignition, carbonates and soluble salts, acid reaction to depth of 38.5 inches, fairly high calcium content, fairly high water-holding capacity for soil containing such high percentage of sand, and a fairly well developed solum to depth of about 38 inches.

CLASSIFICATION OF TEST AREAS INTO TYPES

Chiefly on the basis of vegetation and topography the test areas included in this paper have been classified into 9 major types. These types have been named according to the chief species in each, which are shown comparatively in Figure 12. Weaver and Fitzpatrick (1934) classified 135 areas of tall-grass prairie into 6 types, 2 of which were climax.

1. *The grama-needlegrass-sedge type* (Figs. 2, 3). Test areas 1, 2, 3, 4, 6, 7, and 36 appear to have sufficient resemblance, especially in species and topography, to be classified in this type. The topography varies from upland plateaus to gentle upland slopes (see Figs. 2, 3). Since the soil has been free from excessive erosion and deposition for a long period, it is usually mature. The vegetation, where protected from excessive grazing, mowing, or other use, has apparently reached stabilization as far as this is possible under the severe climatic fluctuations. In years of favorable rainfall, the cover is fairly dense.

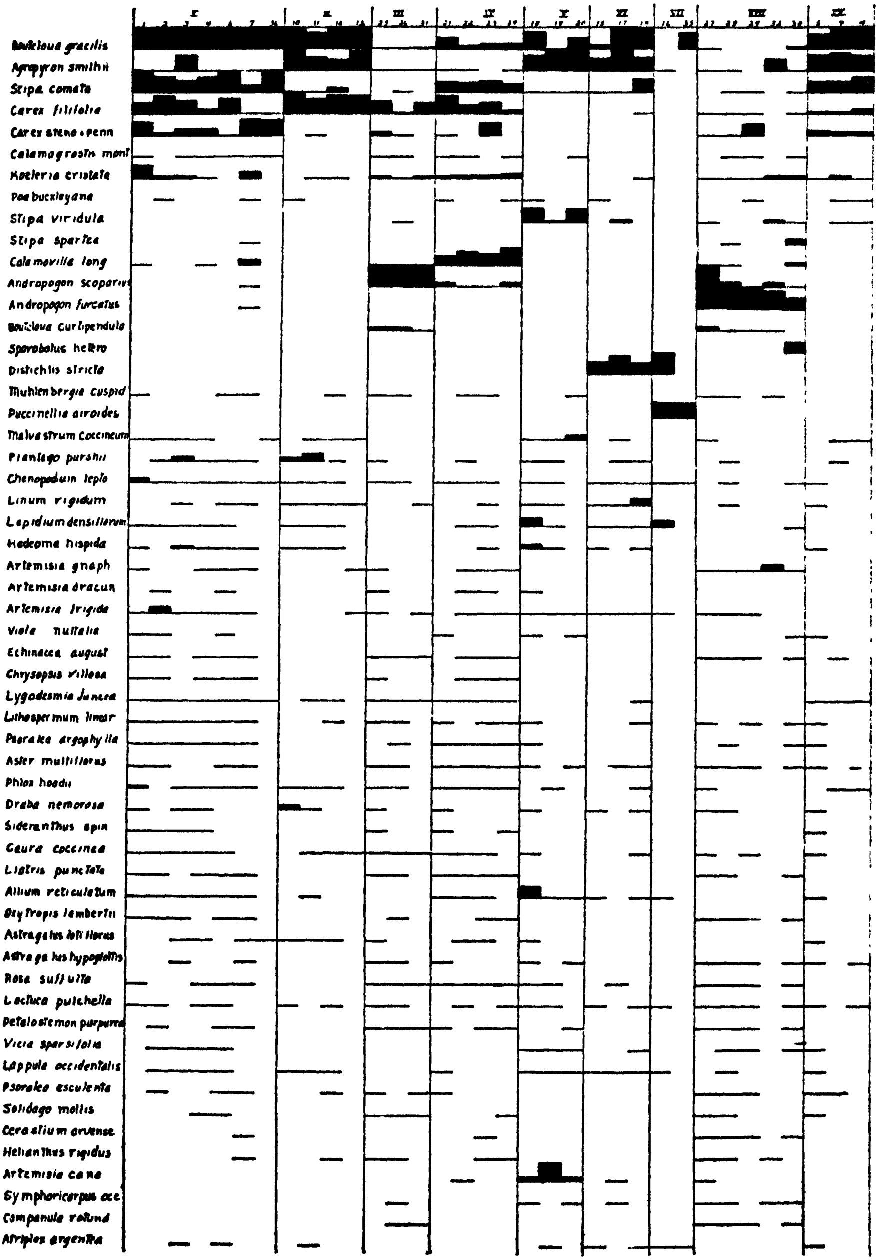

FIG. 12. The importance of 57 of the leading species is shown comparatively for test areas and types. Each species is given 10 small horizontal spaces. Each small vertical space has a F x A value of 10. In area 1 *Bouteloua gracilis* occupies 10 horizontal spaces so it has an F x A value of 100, but in area 11 it has a F x A value of 75 so it occupies 7.5 vertical spaces. *Bouteloua gracilis* is absent on 5 areas. Most of the species have such low F x A values that lines alone are used to indicate their presence.

TABLE 3. Characteristics of soils according to horizons described in soil profile descriptions for each type.

Horizon	Mechanical Composition					Moisture holding capacity, percent	Loss on ignition, percent	pH	Carbonates, percent	Total soluble salts, P.P.M.	Morgan's Universal System Tests*					
Inches	Sands, percent	Silt, percent	Clay, percent	Finer clay, percent	Total colloids, percent						Nitrate N	Ca	P	Na	K	Cl
TEST AREA 1 Bouteloua, Stipa, Carex																
1 — 7	74.0	13.7	12.3	12.1	16.8	49.6	4.92	6.46	1.9	557	2	2,000	25+	0	400	0
7 —17	76.8	13.9	9.3	12.0	16.3	44.3	3.00	6.65	2.3	680	0	3,000	25+	0	150	0
17 —20.5	77.7	13.2	9.1	18.8	15.5	44.8	3.36	7.80	2.6	484	0	3,000	25+	0	150-	0
20.5—32	76.3	14.2	9.5	12.6	17.1	45.3	4.80	8.09	7.5	424	0	3,000	50	0	150--	0
32 —40	76.7	13.4	9.8	11.6	16.7	44.0	3.47	8.02	14.8	544	0	3,000	25	0	150	0
Ave. to W D 40 in	76.3	13.8	9.9	12.6	16.7											
TEST AREA 2 Bouteloua, Carex, Stipa.																
1 — 5.5	71.8	20.4	7.8	6.6	11.9	55.9	5.68	6.75	2.2	473	0	2,000	10	0	600	0
5.5 —13	71.5	18.2	10.3	8.3	13.1	50.9	4.77	7.43	1.7	398	0	2,000	10—	0	500	0
13 —23	60.0	26.0	14.0	10.3	18.0	52.9	3.70	7.70	3.1	476	0	2,000	T	0	200	0
23 —31	55.7	26.0	18.3	16.6	22.0	57.9	5.31	7.97	4.8	473	0	2,000	0	0	150	0
31 —42	52.9	27.9	19.2	16.4	24.6	52.8	7.27	8.04	8.7	600	0	1,000	0	0	150	0
Ave to W D 36 in	62.0	23.9	14.1	11.7	18.0											
TEST AREA 3 Bouteloua, Agropyron, Carex, Stipa.																
1 — 4	31.4	43.5	25.1	22.8	31.8	64.0	6.47	6.01	6.1	577	T	1,000	100	0	200	T
4 — 9	32.5	38.3	29.2	25.8	33.3	58.1	5.08	5.92	7.8	480	T	1,000	100	0	150	T
9 —14	31.6	40.6	27.8	25.8	34.3	60.9	4.71	6.35	8.7	414	T	2,000	100+	0	T	T
14 —24	28.7	39.0	32.3	28.5	38.9	58.2	6.20	8.11	24.2	553	T	3,000	50	0	T	0
Ave. to W D 24 in	30.5	39.8	29.7	26.6	35.7											
TEST AREA 4. Bouteloua, Stipa, Carex.																
0.5— 2.5	63.1	22.6	14.3	11.7	19.7	54.9	6.22	5.78	8.3	334	T	2,000	100	0	400	T
2.5— 6	63.9	20.9	15.2	11.9	20.0	55.2	4.47	5.82	7.7	359	T	2,000	100	0	200	0
6 —15	62.7	17.8	19.5	17.3	23.7	48.9	3.77	6.38	8.6	324	T	2,000	50	0	150	0
15 — 22.5	64.3	16.7	19.0	16.0	22.9	49.6	3.46	6.45	6.4	551	T	2,000	50	0	T	0
22.5—33	64.9	14.2	20.9	18.8	24.4	51.7	3.46	6.82	7.9	382	T	1,000	100	0	T	0
33 —43	70.9	10.3	18.8	17.9	21.4	50.7	2.95	7.18	4.6	390	T	1,000	100	0	T	0
43 —50.5	76.4	4.5	19.1	16.8	20.8	42.1	2.60	7.56	3.9	411	2	3,000	200	0	T	0
Ave to W D 40 in	63.8	17.5	18.7	16.6	22.9											
TEST AREA 5. Bouteloua, Agropyron, Stipa, Carex																
0 — 2	55.0	31.5	13.5	9.7	19.1	55.0	6.77	7.04	7.7	428	0	2,000	50	0	600	0
2 — 7	54.7	27.4	17.9	15.5	23.8	53.7	6.45	6.85	8.3	476	0	2,000	10	T	150	0
7 —21	32.9	40.3	26.8	23.4	33.2	50.8	6.72	8.21	17.0	419	0	1,000	10	T	150	0
21 —30	52.2	25.7	22.1	18.8	27.6	50.0	6.30	8.38	15.6	499	0	1,000	10	T	150	T
30 —33	33.8	34.4	31.8	23.0	39.5	54.7	5.29	8.06	15.7	3,250	0	2,000	10	T	150	8
33 —38	16.9	50.0	33.1	8.6	57.3	66.9	10.60	7.53	16.6	5,500	0	2,000	10	1,000	150	8
38 —59	30.8	45.8	23.4	9.4	38.1	56.8	8.62	7.62	20.8	6,300	0	2,000	25	1,000	150	8
Ave. to W D 28 in	43.3	33.6	23.1	21.9	29.1											
TEST AREA 6. Bouteloua, Stipa, Carex.																
1 — 3.5	70.2	18.8	11.0	8.3	14.2	54.8	5.09	5.79	7.8	375	0	1,000	10	0	200	0
3.5—13	73.9	13.7	12.4	10.6	14.9	61.7	3.61	5.92	7.9	379	0	1,000	10	0	200	0
13 —22	81.8	9.0	9.2	7.9	12.6	47.3	2.84	6.92	7.4	383	0	1,000	10	0	150—	0
22 —34	82.8	5.8	11.4	8.7	13.2	45.3	2.97	8.02	10.6	454	0	1,000	10	0	T	0
34 —44	87.0	5.5	7.5	6.3	8.5	39.4	1.71	8.21	10.9	451	0	1,000	25	0	150—	0
Ave. to W.D.29.5 in	78.4	10.6	11.0	9.1	13.7											

*Figures refer to approximate pounds per acre.

TABLE 3. (Continued).

Horizon	Mechanical Composition					Moisture holding capacity, percent	Loss on ignition, percent	pH	Carbonates, percent	Total soluble salts, P. P. M.	Morgan's Universal System Tests*					
Inches	Sands, percent	Silt, percent	Clay, percent	Finer clay, percent	Total colloids, percent						Nitrate N	Ca	P	Na	K	Cl
TEST AREA 7. Bouteloua, Carex, Koeleria, Calamovilfa, Stipa.																
1.5— 3	58.2	27.5	14.3	11 7	19 7	64 8	6.77	6 18	7 8	360	0	2,000	50	0	200	0
3 — 7.5	57.3	26 0	16 7	14.1	23.1	62.8	5.99	6.18	8 3	408	0	1,000	25—	0	T	0
7 5—18	65.6	18.0	16.4	13.6	19 6	53.4	4 04	6 43	7 8	514	0	1,000	25	T	T	0
18 —27	71.7	14.2	14.1	12 9	16 8	49 4	3 16	6 84	8.3	439	2	1,000	50	0	T	0
27 —38	70.2	14 0	15 8	14 3	18 6	45 3	3 15	7 11	7.9	318	0	750	25	0	T	0
38 —44	76 3	11.3	12 4	10.6	15 0	42 6	3.60	8 11	7 6	281	0	2,000	50	0	T	T
44 —60	87.0	6.2	6 8	5 7	8 9	38 7	2 13	8 38	7 2	283	0	1,000	25	0	T	0
Ave. to W.D. 33 in.	66.7	17.8	15.5	13.5	19 0											
TEST AREA 8. Bouteloua, Agropyron, Stipa																
1 —10	18 7	32.6	48 7	42 7	59 4			6 80								
10 —18	21 8	31.3	46.9	41.6	56 0			7.75								
18 —34	21 7	33 2	45.1	39 0	55 7			8 02								
34 -53	35 8	27.0	37 2	32 8	45.1			8.31								
53 —66	73 9	14 4	11 7	11 2	13 8			8 50								
Ave. to W.D 34 in.	20 9	32 6	46 5	32 5	44.8											
TEST AREA 10. Agropyron, Bouteloua, Carex.																
1 — 4 5	34 8	41 3	23 9	20 2	33 3	60 5	7.8	7 36	7 4	692	T	2,000	17	0	150	0
4 5—10 5	37.3	32 2	30 5	26 7	38 8	60.7	10 6	7 87	25 9	626	0	2,000	10—	0	150	0
10 5—27	29 7	35.0	35 3	29 5	40 3	51 9	9 5	8.38	31 4	634	0	2,000	10 -	0	150-	0
27 —45	33 5	29 8	36 8	17 2	43 8	39.8	17 7	8.63	31.2	236	0	2,000	10	2,000	150 -	T
Ave. to W D 25 in.	32 4	35 2	32 4	22 5	38 9											
TEST AREA 11. Agropyron, Bouteloua, Carex.																
0 — 1 5	32.6	49.8	17 6	15 3	29.0	84 7	11 6	7.20	8 3	626	20	2,000	50	T	600	0
1.5— 3 5	30 1	44 9	25 0	18 3	33 7	68 8	8 1	7.30	8.3	520	2	3,000	25	T	600	0
3.5 – 7.5	38 4	38.0	23 6	18 4	30 9	57 1	4 9	7 50	11 0	604	0	2,000	25	0	150	0
7.5—14	20 6	44 7	34 7	30 1	46.7	61.0	7.2	7 70	8.9	648	0	2,000	25	T	150—	T
14 --26	23 7	40 5	35 8	30 8	45.1	63 0	4.7	7 80	14 0	553	0	3,000	10	0	150	0
26 —47 5	39 5	33 8	26 7	24.2	32 4	53 1	4 0	7.90	19 2	559	0	3,000	10	0	150—	T
47.5—62	46 4	30.7	22.9	19 7	26.9	48 0	2 6	8.00	15.0	1,538	0	2,000	0	0	150—	T
Ave. to W.D 35 in.	29.6	39 9	30 5	25 2	38 2											
TEST AREA 12 Bouteloua, Agropyron, Carex.																
0 5— 2	62 0	25.8	12 2	9 8	16.1	60 0	6.9	6.8	8 6	492	T	1,000	50	0	150	0
2 -- 6	46.5	31 1	22 4	19 4	28.7	59.2	6.7	6.6	7.2	608	T	750+	50	0	T	0
6 —10	44.0	32 6	23 4	19 8	30 9	54.8	7 1	8.2	17.3	596	T	750	50	0	T	0
10 —20	39 7	31 8	28 5	25 2	37.2	54 2	6 0	8 3	22.0	566	T	750+	50	T	T	T
20 —27	25.1	36.4	38 5	32.5	46 2	57 5	10 2	8 4	19.9	568	T	750	100	T	T	T
27 —40	29 1	38 3	32 6	29.0	41 3	54 4	6 9	8 4	22 7	618	T	750	50	T	T	T
Ave. to W.D. 32 in.	37.2	33.6	29 2	24 9	36.4											
TEST AREA 13. Bouteloua, Agropyron, Carex.																
1.5—15	32.5	37.3	30 2	25.9	28.2			7.5								
15 —21	29.4	37.2	33.4	28 4	44 1			7.8								
21 —37	30.0	40 9	29 1	25 1	37 9			8.0								
37 —50	33.6	40 3	26.1	18.7	35.1			8.2								
Ave. to W.D. 28 in.	31 1	38 3	30 6	24 8	37.4											

*Figures refer to approximate pounds per acre.

TABLE 3. (Continued).

Horizon	Mechanical Composition					Moisture holding capacity, percent	Loss on ignition, percent	pH	Carbonates, percent	Total soluble salts, P. P. M.	Morgan's Universal System Tests*					
Inches	Sands, percent	Silt, percent	Clay, percent	Finer clay, percent	Total colloids, percent						Nitrate N	Ca	P	Na	K	Cl
TEST AREA 14. Bouteloua, Agropyron, Stipa, Distichlis.																
0 — 1	56.9	24.9	18.2	15.9	24.0	56.7	7.1	7.28	20.1	592	T	2,000	50	T	200	0
1 — 3	60.6	25.3	14.1	14.2	21.3	53.9	6.0	7.18	18.2	463	T	2,000	25	T	150	0
3 — 7	66.9	15.0	18.1	15.6	21.5	47.5	3.9	7.70	18.3	470	0	2,000	25	0	200	0
7 — 8.5	65.7	16.5	17.8	14.3	22.2	51.3	3.3	7.77	16.4	592	0	1,000	10	0	200	0
8.5 —15.5	65.6	20.2	14.2	11.0	17.0	26.8	4.9	8.00	16.9	1,276	0	2,000	25	T	400	0
15.5—40	60.3	23.0	16.7	15.1	20.0	49.1	2.9	8.40	17.0	5,200	0	2,000	10	1,500	300	T
40 —49	Coarse scoria in heavy clay					53.6	3.0	8.60	16.5	4,600	0	1,000	10	1,500	150	T
49 —54	52.5	28.7	18.8	16.6	22.5	52.0	4.1	8.70	23.1	3,500	0	2,000	25	1,500	150—	8
Ave. to W.D. 26 in.	62.9	20.9	16.2	14.5	20.5											
TEST AREA 15. Agropyron, Distichlis																
0 — 3	38.9	44.7	16.4	13.1	26.9	59.3	10.2	7.50	18.0	915	10	4,000	50	0	200	T
3 — 4	30.3	42.0	27.7	12.2	29.3	86.9	12.4	7.60	12.1	746	2	3,000	50	0	400	T
4 — 6	26.1	57.4	16.5	12.8	30.5	67.1	7.0	7.60	16.8	749	T	3,000	25	0	150	T
6 — 11.5	26.2	56.3	17.5	13.8	29.8	61.8	9.7	7.70	19.8	3,550	T	2,000	25	T	150—	T
11.5—20.5	27.6	56.5	15.9	12.5	27.7	61.4	7.2	7.80	19.4	4,800	T	2,000	25	150	T	T
20.5—51	39.8	40.7	19.5	15.5	27.7	55.8	4.5	8.30	18.0	4,800	T	2,000	25	150	T	T
Ave. to W.D. 22 in.	29.5	53.2	17.3	13.4	28.4											
TEST AREA 16. Distichlis, Puccinellia																
0 — 4.5	41.3	40.8	17.9	14.4	27.0	58.2	4.8	7.70	17.6	1,587	0	3,000	25	T	T	0
4.5 —15.5	22.5	53.2	24.3	17.4	28.3	59.3	6.6	8.10	18.6	11,100	2	3,000	25	200	T	0
15.5—35.5	21.5	48.8	29.7	25.3	40.7	60.6	7.0	8.20	21.5	8,500	T	3,000	25	200—	0	0
35.5 —54	32.6	43.4	25.0	22.1	33.2	55.3	4.8	8.30	21.5	4,300	T	3,000	50	200	T	0
Ave. to W.D. 18 in.	27.0	49.5	23.5	15.5	35.8											
TEST AREA 17. Agropyron, Distichlis, Bouteloua.																
0 — 2	57.0	28.7	14.3	11.9	19.6	47.4	6.6	7.16	14.5	603	0	2,000	0	0	600	0
2 — 6	52.1	32.1	15.8	13.2	22.9	46.6	5.0	7.28	15.6	660	0	1,000	0	0	600	0
6 —20	48.0	35.4	16.6	14.1	22.6	48.2	5.6	7.53	16.0	875	0	1,000	0	0	150—	0
20 —31	38.9	44.1	17.0	16.4	30.0	52.8	7.2	7.90	14.0	4,800	0	2,000	0	1,500	150	0
31 —66	57.0	25.7	17.3	10.3	21.9	44.3	3.7	8.00	16.9	7,200	0	2,000	0	1,500	150—	0
Ave. to W.D. 39 in.	48.2	35.1	16.7	13.8	24.4											
TEST AREA 18. Artemisia cana, Bouteloua, Agropyron, Stipa viridula																
0 — 2	23.1	46.9	30.0	21.9	42.2	68.5	13.4	7.60	9.7	637	0	3,000	50	0	600	T
2 — 7	15.0	46.7	38.3	30.0	50.7	71.9	11.1	7.70	8.7	595	0	3,000	50	0	200	0
7 —11	12.9	43.8	43.3	36.6	60.2	69.8	12.8	7.70	8.8	870	0	3,000	25	T	150—	0
11 —18	16.2	48.2	35.6	28.8	50.3	61.0	6.6	7.70	13.5	688	0	2,000	25	0	150—	0
18 —27	20.1	47.2	32.7	27.5	44.3	56.9	8.3	7.70	15.2	537	0	2,000	10	0	150—	0
27 —61	16.6	46.1	37.3	32.3	49.4	60.6	6.6	7.70	16.0	910	0	2,000	10	0	150—	0
Ave. to W.D. 31 in.	17.1	46.8	36.1	29.0	49.2											
TEST AREA 19. Artemisia cana, Agropyron.																
0.5—12.5	37.0	50.6	12.4	11.4	21.2	44.9	5.4	7.70	15.9	812	0	2,000	0	T	150—	0
12.5—48.5	12.2	64.2	23.6	8.7	43.2	54.5	3.5	7.70	15.9	1,284	0	1,000	0	T	150—	0
48.5—53	63.3	28.1	8.6	7.7	12.4	40.4	7.4	7.26	14.3	1,050	2	2,000	0	1,000	150	T
53 —64	36.6	49.7	13.7	12.3	18.0	47.5	2.4	7.94	17.6	1,220	20	1,000	0	1,000	150	0
Ave. to W.D. 52 in.	21.4	58.6	20.0	9.4	36.2											

*Figures refer to approximate pounds per acre.

TABLE 3. (Continued).

Horizon	Mechanical Composition					Moisture holding capacity, percent	Loss on ignition, percent	pH	Carbonates, percent	Total soluble salts, P. P. M	Morgan's Universal System Tests*					
Inches	Sands, percent	Silt, percent	Clay, percent	Finer clay, percent	Total colloids, percent						Nitrate N	Ca	P	Na	K	Cl
TEST AREA 20 Artemisia cana, Agropyron, Stipa viridula, Bouteloua.																
2.5—10	15.6	25.8	58.6	51.9	69.7			7.53								
10—18.5	21.2	39.5	39.3	33.3	51.9			8.13								
18.5—25.5	16.3	62.3	21.4	16.4	29.6			7.86								
25.5—40.5	78.2	14.8	7.0	6.5	9.7			8.23								
Ave. to W.D. 42 in.	41.7	30.9	27.4	23.5	35.8											
TEST AREA 21. Calamovilfa.																
0—6	87.3	9.4	3.3	3.1	5.1	40.9	3.4	7.50	15.2	378	0	1,000	25	0	T	0
6—74	76.0	16.3	7.7	5.9	10.9	41.5	2.6	7.70	16.1	494	T	2,000	25	0	T	0
Ave. to W.D. 70 in.	77.0	15.7	7.3	5.7	10.4											
TEST AREA 22. Calamovilfa, Carex.																
1.5—3.5	76.7	16.2	7.1	5.5	11.1	51.8	4.1	6.11	6.5	377	0	1,000	50	0	600	0
3.5—8.5	79.9	12.8	7.3	6.8	12.2	48.1	3.2	6.28	6.8	370	0	1,000	25	0	600	0
8.5—13	78.3	9.8	11.9	8.6	15.9	45.8	2.5	6.26	6.2	374	0	1,000	25	0	600	0
13—19	78.3	13.3	8.4	7.0	12.5	43.8	2.6	6.43	7.2	327	0	1,000	25	0	150	0
19—24	79.8	8.5	11.7	9.2	13.0	43.8	2.1	6.52	6.7	364	0	1,000	10	0	150	0
24—69	78.8	12.2	9.0	8.0	11.8	44.3	2.4	6.52	6.0	569	0	1,000	10	0	150	T
Ave. to W.D. 56 in.	78.7	12.1	9.2	7.8	12.3											
TEST AREA 23. Calamovilfa, Carex, Stipa																
0—3	76.4	15.0	8.6	6.5	12.4	52.3	4.5	6.31	7.5	284	0	1,000	25	0	500	0
3—8	73.6	13.7	12.7	9.7	15.6	48.7	3.8	6.18	5.9	327	0	1,000	10	0	150—	0
8—17.5	71.7	15.1	13.2	12.4	16.9	52.4	3.0	6.48	6.8	436	0	750	10	0	T	0
17.5—26.5	69.2	16.6	14.2	12.1	18.2	52.6	2.4	6.50	7.0	391	0	1,000	10	0	150—	0
26.5—42	66.4	17.1	16.5	15.0	20.6	51.7	2.4	6.85	4.2	588	0	750	10	0	150—	0
42—60	60.2	21.0	18.8	16.8	23.4	52.1	3.1	7.34	6.2	252	0	1,000	10	0	T	0
Ave. to W.D. 57 in.	67.3	17.3	15.4	13.7	19.5											
TEST AREA 24. Calamovilfa, Carex																
1.5—23	69.3	16.6	14.1	12.1	18.9			6.48								
23—39	74.4	13.9	11.7	10.1	14.4			6.50								
39—61	74.0	11.9	14.1	11.8	16.5			7.04								
61—72	77.7	9.4	12.9	11.5	14.7			7.47								
Ave. to W.D. 58 in.	72.4	14.3	13.3	11.2	16.4											
TEST AREA 25 Andropogon scoparius.																
0—1.5	66.9	27.1	6.0	4.6	9.3	52.5	6.22	7.20	7.1	406	2	1,000	25	0	T	0
1.5—4	50.3	36.4	13.3	13.5	22.4	64.7	8.10	7.40	21.7	463	T	2,000	25	0	T	0
4—7	22.7	53.6	23.7	17.0	33.5	64.3	8.17	7.60	23.8	672	0	3,000	25	0	0	0
7—12	9.0	54.8	36.2	29.8	54.5	63.4	8.26	7.70	30.0	506	0	2,000	25	0	T	0
12—20	25.0	59.2	15.8	12.8	26.0	54.2	7.10	7.80	26.0	517	0	3,000	10	T	150—	0
20—37	30.5	60.8	8.7	6.6	16.4	53.2	1.90	7.90	25.9	312	0	3,000	10	T	T	0
37—53	18.0	71.9	10.1	7.5	21.5	52.3	5.52	7.90	28.5	629	0	2,000	25	0	T	0
Ave. to W.D. 26 in.	28.0	54.0	18.0	13.7	28.8											
TEST AREA 26. Andropogon scoparius.																
1—5	24.8	56.9	18.3	15.5	30.5	68.2	8.53	7.40	19.6	630	T	2,000	25	0	T	T
5—9.5	16.9	54.8	28.3	23.9	40.1	64.3	8.40	7.70	23.5	743	T	3,000	25	0	T	0
9.5—18	17.7	52.2	30.1	23.8	42.1	61.8	5.15	7.90	22.9	559	T	2,000	25	0	T	0
18—23.5	40.1	40.5	19.4	16.2	27.4	58.8	4.68	8.20	22.4	387	T	2,000	25	0	T	0
23.5—53	26.9	47.6	25.5	19.5	34.0	55.7	4.50	8.40	26.1	584	T	2,000	25	0	0	0
Ave. to W.D. 48 in.	25.6	49.1	25.3	19.9	35.0											

*Figures refer to approximate pounds per acre.

TABLE 3. (Continued).

Horizon	Mechanical Composition					Moisture holding capacity, percent	Loss on ignition, percent	pH	Carbonates, percent	Total soluble salts, P. P. M.	Morgan's Universal System Tests*					
Inches	Sands, percent	Silt, percent	Clay, percent	Finer clay, percent	Total colloids, percent						Nitrate N	Ca	P	Na	K	Cl
TEST AREA 27. Andropogon furcatus.																
0 — 3	50.0	41.5	8.5	7.1	13.8	72.5	10.15	6.94	13.3	566	2	1,000	50	0	T	0
3 — 6	46.7	39.6	13.7	12.2	20.6	76.6	8.70	6.87	11.8	541	2	1,000	50	0	0	0
6 —12	43.3	42.1	14.6	12.1	21.5	71.9	8.78	6.72	11.7	642	T	1,000	50	0	0	T
12 —20	45.9	40.1	14.0	11.6	19.7	62.3	7.68	7.01	10.3	543	0	2,000	50	0	0	0
20 —36	46.1	38.1	15.8	12.7	21.9	63.6	8.28	7.29	8.2	377	0	2,000	50	0	0	0
36 —41	44.9	34.7	20.4	17.5	27.6	56.2	9.60	8.00	17.9	364	T	3,000	25	0	0	0
41 —48	49.9	30.1	20.0	17.6	26.1	52.0	8.98	8.20	20.1	548	T	3,000	25	0	0	T
Ave. to W D 46 in	46.2	38.1	15.7	13.1	21.9											
TEST AREA 28 Andropogon furcatus																
1.5 — 4	44.6	36.2	19.2	15.5	26.6	99.6	13.65	5.50	8.4	496	0	1,000	25	0	150	0
4 — 9	31.7	40.8	27.5	23.2	34.7	72.9	7.61	5.84	9.3	678	0	1,000	25	0	200	0
9 —13	30.9	35.8	33.3	29.8	42.3	72.3	6.16	5.99	8.4	670	0	1,000	10	0	150—	0
13 — 17.5	43.6	31.0	25.4	21.6	32.5	65.1	5.27	6.28	9.0	612	0	750	25	T	150 —	0
17.5—25	45.5	37.6	16.9	14.0	21.6	57.1	4.31	7.11	12.8	509	0	1,000	T	0	T	0
25 — 39	41.9	45.2	12.9	10.8	18.3	59.6	4.02	7.24	17.0	622	0	750	10	T	T	0
Ave. to W. D. 33.5 in	40.6	38.5	20.9	17.8	27.2											
TEST AREA 29 Andropogon furcatus.																
1 — 4	55.7	29.0	15.3	13.1	21.1			7.41								
4 —15	49.2	36.1	14.7	11.9	22.7			7.73								
15 —22	32.6	42.2	25.2	19.1	34.8			8.00								
22 —41	6.7	30.3	63.0	53.1	79.1			8.03								
Ave. to W.D 41 in	25.9	35.5	38.6	32.0	50.2											
TEST AREA 30 Sporobolus, Andropogon																
1 — 4	61.7	34.4	3.9	2.8	8.2	91.6	12.20	6.35	5.5	406	0	2,000	25	0	600	0
4 — 11	65.1	26.4	8.5	7.0	15.0	60.4	5.80	6.60	5.7	369	0	2,000	25	T	600	0
11 —18	69.5	23.6	6.9	5.1	13.0	57.3	5.10	6.67	5.5	377	0	2,000	25—	0	600	0
18 — 28	71.2	18.0	10.8	8.0	15.7	54.3	3.63	6.60	7.3	275	0	1,000	10	T	300	0
28 — 33	76.2	12.3	11.5	8.9	15.2	51.2	3.80	7.50	8.6	322	0	1,000	10	T	150—	0
33 —54	75.9	10.3	13.8	11.8	17.5	48.7	3.70	8.00	18.1	374	0	2,000	10 -	T	150—	0
Ave. to W.D. 38 in.	70.2	20.2	9.6	7.7	14.6											
TEST AREA 31. Andropogon scoparius																
1.5—4.5	43.3	37.1	19.6	16.5	26.0	63.9	6.87	7.53	21.1	572	T	3,000	50	0	T	0
4.5—12	45.2	39.0	15.8	13.2	22.0	62.5	6.50	7.89	25.1	622	T	3,000	25	0	T	0
12 —17	29.1	43.2	27.7	21.1	36.4	59.4	8.03	8.11	30.9	566	60	3,000	25	0	T	0
17 —23	28.6	47.1	24.3	19.8	33.5	57.8	7.90	8.21	30.1	444	40	3,000	25+	T	T	0
23 —45	31.5	43.5	25.0	19.9	32.8	51.6	6.10	8.12	30.9	570	10	3,000	50+	0	T	0
Ave. to W.D. 42 in.	34.2	42.7	23.1	18.0	30.1											
TEST AREA 32. Andropogon furcatus.																
1 — 3	31.5	54.2	14.3	12.4	24.7	89.0	11.60	6.41	7.4	430	0	1,000	25	0	150	0
3 —10	52.5	36.1	11.4	8.6	16.7	74.9	6.57	6.52	7.2	329	0	1,000	25	0	150—	0
10 — 21	47.7	39.6	12.7	8.8	18.9	73.7	7.59	6.52	6.4	492	0	1,000	10	0	150—	0
21 —25.5	50.5	32.0	17.5	14.6	24.1	62.2	4.55	6.67	6.7	492	0	1,000	25	0	150—	0
25.5—32	56.2	29.4	14.4	11.9	19.6	56.6	4.69	6.87	10.2	436	0	1,000	10	0	150—	0
32 —40	46.1	36.6	17.3	14.6	24.2	62.2	5.57	7.80	9.0	401	0	1,000	25	0	150—	0
40 —46	50.2	34.5	15.3	12.6	21.5	57.9	4.26	7.97	15.1	332	0	1,000	10	0	T	0
46 —49	50.2	25.4	24.4	20.7	30.8	59.0	5.95	8.38	27.8	443	0	750	10	0	T	0
Ave. to W.D. 36 in.	49.5	36.5	14.0	10.9	20.2											

*Figures refer to approximate pounds per acre.

TABLE 3. (Continued).

Horizon	Mechanical Composition					Moisture holding capacity, percent	Loss on ignition, percent	pH	Carbonates, percent	Total soluble salts, P. P. M.	Morgan's Universal System Tests*					
Inches	Sands, percent	Silt, percent	Clay, percent	Finer clay, percent	Total colloids, percent						Nitrate N	Ca	P	Na	K	Cl
TEST AREA 33. Buchloe.																
1 —7	22.4	34.8	42.8	35.4	54.2	60.3	5.87	7.40	6.3	1,002	0	1,000	25	0	150	0
7 —13.5	15.1	40.3	44.6	37.7	60.9	57.2	6.40	7.80	9.0	1,332	0	2,000	25	0	150-	0
13.5—25	17.0	32.8	50.2	42.1	62.2	57.3	6.22	7.70	9.5	1,184	T	2,000	50	0	T	0
25 —32	63.6	11.2	25.2	22.0	29.3	46.8	2.95	7.70	7.2	628	0	750	25	T	150	0
32 —42	41.8	20.9	37.3	31.6	45.4	57.3	4.30	7.80	7.7	2,456	0	1,000	50	T	T	0
Ave. to W.D. 33 in.	28.6	29.6	41.8													
TEST AREA 34 Bouteloua, Poa buckleyana																
1.5— 7	32.2	43.3	24.5	17.9	34.3	60.1	7.87	6.41	5.8	392	T	3,000	10	0	200	0
7 —14	25.6	37.7	36.7	21.3	47.6	59.5	6.10	6.67	6.7	840	0	2,000	10+	0	T	0
14 —23	19.2	47.6	33.2	28.2	45.9	59.3	5.82	6.79	7.0	761	0	2,000	10+	0	150	0
23 —30.5	29.7	33.9	36.4	29.9	47.4	57.7	5.62	7.46	7.3	719	0	2,000	10	T	T	0
30.5 —55	33.8	31.6	34.6	29.0	43.8	57.4	5.07	8.10	8.2	1,074	0	2,000	10	T	T	T
Ave. to W.D. 33 in.	26.6	40.1	33.3													
TEST AREA 35 Distichlis, Puccinellia, Agropyron.																
0 —1.5	52.5	38.5	9.0	6.7	16.4	Would	2.65	6.77	5.0	354	T	400	50	1,000	600+	0
1.5— 4	47.7	34.7	17.6	16.3	22.7	not	3.67	7.20	7.0	1,943	T	400-	50	2,000	600	0
4 — 8	29.2	39.8	31.0	27.9	37.1	take	4.53	8.60	8.9	13,500	2	1,000	100	6,000	600	0
8 —14	25.7	55.2	19.1	17.4	43.7	water	4.80	8.50	9.9	13,900	T	1,000	100	5,000	600	T
14 —19	13.2	41.8	45.0	42.5	56.3	61.4	5.95	8.10	11.1	11,300	0	2,000	50	6,000	600	0
19 —37	14.3	29.2	56.5	50.2	66.8	63.1	5.55	7.70	7.5	11,200	0	1,000	50	5,000	300	0
37 —42	26.3	36.9	36.8	33.6	48.4	60.0	4.95	7.70	10.0	9,600	0	1,000	25	4,000	200	0
Ave. to W.D. 26 in.	24.4	40.3	35.3	31.9	47.7											
TEST AREA 36. Bouteloua, Stipa.																
1.5— 4.5	56.2	24.9	18.9	16.7	24.9	60.9	6.25	6.01	6.2	378	T	1,000	25	0	500	0
4.5 —12	63.7	17.4	18.9	17.6	21.9	51.6	3.92	6.36	6.4	322	T	2,000	25	T	150	0
12 —19.5	68.0	12.3	19.7	18.8	22.2	47.2	3.40	6.28	7.1	386	0	2,000	50	T	150-	0
19.5—29	61.0	17.5	21.5	19.7	24.8	50.3	3.25	6.43	6.9	473	0	2,000	25	0	150-	0
29 —38.5	65.9	15.5	18.6	16.9	21.1	48.5	3.10	6.50	6.8	472	0	2,000	10+	0	T	0
38.5—41.5	67.1	14.2	18.7	16.9	21.1	47.4	2.80	7.70	7.8	440	0	3,000	10	0	T	0
41.5—51	62.1	18.3	19.6	17.7	22.5	50.8	3.75	8.00	9.6	465	T	2,000	25	0	T	T
51 —57	75.1	10.5	14.4	13.0	16.2	46.4	2.75	8.14	8.8	518	0	2,000	25	0	T	0
Ave. to W.D. 51 in.	63.7	16.7	19.6													

*Figures refer to approximate pounds per acre.

The frequency-abundance figures are useful in evaluating the relative importance of species in the type. The average and range in these figures for test areas 1, 2, 3, 4, 6, and 7, are for *Bouteloua gracilis* 96.5 (90.7-100), *Stipa comata* 68.6 (29.0-97.7), *Carex filifolia* 52.2 (0.2-100), *Carex stenophylla* (including some *C. pennsylvanica*) 35.3 (8.7-69.3), *Koeleria cristata* 16.3 (0-47.5), and *Agropyron smithii* 15.3 (0.3-66.3). All other species rated much lower, as for example, the more abundant characteristic forbs, *Malvastrum coccineum* 1.7 (0-5.7), *Chenopodium leptophyllum* 4.6 (0.8-15.9), *Lygodesmia juncea* 0.9 (0.1-2.6), *Plantago purshii* 3.7 (0-18.4),

Lepidium densiflorum 1.6 (0-4.4), *Hedeoma hispida* 1.4 (0-6.2), *Artemisia gnaphalodes* 5.2 (0-14.7), *Artemisia frigida* 7.1 (0.1-40.0), *Echinacea angustifolia* 0.9 (0-2.8), *Psoralea argophylla* 0.6 (0.1-2.1), *Gaura coccinea* 0.3 (0-0.9), and *Allium reticulatum* 1.5 (0-7.0). These figures indicate that the chief dominants are the first three grasses listed. Since the other three grasses have high frequency-abundance figures on some areas they should also rank as dominants but of less importance than the first three.

Except for *Bouteloua gracilis* considerable variation usually occurs in the frequency-abundance of each species on different areas in this type. The variation in *Stipa comata* appears to be partly due to replacement by other species as *Stipa spartea*, Calamovilfa, *Koeleria cristata*, and *Andropogon scoparius* in test area 7 where *Stipa comata* had a F x A figure of only 29.0. The brown soil extended to 38 inches in area 7 as compared to about 17 inches in area 1 and the moisture holding capacity was considerably higher in the surface layers in the former. Both of these conditions would be favorable to the more mesophytic species. *Carex filifolia* rated only 0.2 in area 7 and 100 in area 2. No explanation appears for this variation except that the greater abundance of taller species in area 7, due probably to more favorable moisture conditions, would handicap *Carex filifolia*. Variations in frequency and abundance of species within a type are due to a variety of causes as effect of competition between species, priority of invasion (the first dominant species to appear on an area, as *Carex filifolia*, may be difficult to replace), differences in soil conditions, and differences in treatment as grazing, mowing, or total protection.

The frequency-abundance figure for forbs (omitting *Draba nemorosa* and *Plantago purshii*) in this type averaged 37, ranging from 22 to 65 in 6 test areas. The high proportion of sand in area 6 is probably one of the causes for the low frequency and abundance of forbs in it as compared with most of the others. The high F x A number (65) of forbs in area 1 was due chiefly to *Chenopodium leptophyllum*, *Artemisia gnaphalodes*, and *Phlox hoodii*. The total number of species in this type was fairly high, averaging 44.7 and ranging from 33 to 53. The average number of species per quadrat averaged 14.6 (range 10.9-19.2). The variation in number of species on different areas within the same type is due to various causes such as successional age, degree of maturity of vegetation and soil, kinds of associated species and effects of resulting competition, former use of the area, and differences in soil or atmospheric factors, especially moisture. Area 3 had the lowest total number of species while area 7 had the highest number. Area 3 had much less sand in the soil, more carbonate, less potassium, shallower dark soil, and greater abundance of *Agropyron smithii* and *Carex filifolia*. It appears that area 7 presented more favorable soil conditions for a variety of species and a combination of dominant species (Bouteloua-*Carex*

stenophylla-Koeleria-Stipa-Calamovilfa) less exclusive in their domination than those on area 3 (Bouteloua-Agropyron-*Carex filifolia*-Stipa).

Characteristics of this type, as disclosed by the present study, may be summarized as follows:

1) Chief dominants: *Bouteloua gracilis, Stipa comata, Carex filifolia.* Less important dominants: *Carex stenophylla, Agropyron smithii, Koeleria cristata.*
2) Topography: Upland plateaus and gentle upland slopes, largely soil from residual material.
3) Moderately high total number of species in each example of the type (average 44.7, range 33 to 53), about three-fourths of these being forbs.
4) Soil texture usually sandy loam, averaging about 68 percent sand (53-87).
5) Fairly deep layer of dark soil ranging from about 17 to 33 inches thick.
6) Moisture-holding capacity of the soil was moderate ranging from 50 to 65 percent near the surface to 39 to about 58 percent in the deeper layers.
7) Loss-on-ignition was low ranging from 2 to 7 percent.
8) Effervescence with HCl began at various depths ranging from 13 to 60 inches below the surface.
9) The soil was usually slightly acid, pH 5.8 to 6.7, from the surface to average depth of 22.4 inches (5.5-38.5).
10) Carbonate contents were usually low to moderate, ranging from 2 to 15 percent.
11) Soil colloids variable, low to moderate, usually 12 to 30 percent.
12) Total soluble salts were low ranging from 281 to 680 p.p.m.
13) The soil was usually free from sodium (water soluble and exchangeable base) as tested by Morgan's Universal System.
14) Profile well developed.

2. *Western wheatgrass-grama-sedge type* (Fig. 4). Test areas 10, 11, 12, and 13 are classed in this type which usually occurs on fairly long, gradual clay slopes (see Fig. 4). Such slopes are common in the region. It appears that these slopes were formed by the deposition in valleys of material eroded from hills and buttes, represented now by remnants. Soil conditions are not stabilized because the slopes are subject to considerable runoff. Erosion proceeds rapidly when the vegetation cover is broken. Clay and silt may be deposited as the runoff from above is slowed up by the vegetation and more moderate slope. Since these slopes are subject to runoff, erosion, and deposition, development of both vegetation and soil is retarded. The density of the vegetation is often sparse, especially in drought years because these slopes tend to become deficient in soil moisture sooner than areas that are more level and contain more sand.

Frequency abundance averaged for *Bouteloua gracilis* 94 (75-100), *Agropyron smithii* 77 (55-100), *Carex filifolia* 81 (66-85) and *Stipa comata* 6 (0-16). Other grasses, as Koeleria, *Poa buckleyana,* and *Muhlenbergia cuspidata,* and one sedge, *Carex stenophylla,* were scarce. The F x A

index figure for forbs was low, ranging from 4 to 16 in the different test areas. The most common forbs were *Plantago purshii, Hedeoma hispida, Malvastrum coccineum, Linum rigidum, Chenopodium leptophyllum, Lepidium densiflorum, Phlox hoodii, Draba nemorosa, Gaura coccinea, Astragalus lotiflorus,* and *Lappula occidentalis.* The frequency-abundance index figures, as well as the percentages of cover secured by the point method, demonstrate that the dominants in the test areas studied in this type were *Bouteloua gracilis, Agropyron smithii,* and *Carex filifolia.* Observation of other areas showed that these three species were the chief dominants in this type.

Area 12 had a larger frequency-abundance of *Stipa comata* and *Koeleria cristata* and lower frequency-abundance of *Agropyron smithii* than the other areas in this type. These differences appear to be related to the greater amount of sand in the surface 10 inches in area 12 (ranging from 44 to 62 percent in area 12, but 20 to 38 percent in areas 10, 11, and 13); to the much lower amount of colloids (16 percent in area 12, but 28 to 33 in areas 10, 11, and 13; to the acid soil reaction (pH 6.6 to 6.8) in the surface 6 inches of area 12 but alkaline (pH 7.2 to 7.5) in the others; and to the smaller quantities of calcium and potassium in area 12.

Characteristics of the western wheatgrass-grama-sedge type are:

1) Dominants: *Bouteloua gracilis, Agropyron smithii, Carex filifolia.*
2) Topography: Fairly long, gradual slopes; valley-fill deposits.
3) Low total number of species ranging from about 20 to 29 in test areas, about three-fourths being forbs.
4) Soil texture usually clay loams, consisting of 30 percent or more of clay and less than 40 percent of sand.
5) Shallow layer of dark soil, 0 to 6 inches.
6) Moisture-holding capacity moderate, usually ranging from about 60 percent near the surface to 40 to 50 percent deeper.
7) Loss-on-ignition was usually moderate, averaging about 6 to 8 percent, but ranging from 2.6 to 17.7 percent.
8) Effervescence with HCl showed at the surface or began only 1 to 3 inches below.
9) The soil was usually alkaline throughout; pH 7.2-7.5 at the surface to 8.0-8.6 in the deeper horizons.
10) Carbonate contents ranged from moderate (7-8 percent) in surface layers to high in lower layers (15-31 percent).
11) Soil colloids high, usually 25 to 50 percent.
12) Total soluble salts were usually low (500-700 p.p.m.) to depths of 3.5-4 feet.
13) The sodium content was usually negligible but was high in the 27 to 45-inch layer in area 10. Calcium was usually medium high, potassium low.
14) Profile shows moderate development.

3. *Little bluestem type* (Figs. 1, 4). Test areas 25, 26, and 31 belong to this type. It occurs on slopes where snow drifts in and on northerly aspects of fairly steep slopes (10 to 20 degrees) of hills and plateaus. This type is widespread especially in the southern part of the Little Missouri Range

region. The soil material on these slopes appeared usually to be of residual origin, but in some cases was formed evidently by deposition.

Little bluestem is one of the first invaders on areas made bare by "step" erosion (see Fig. 4). Once established it is difficult for other grasses to displace it because of its dense and tall growth as long as soil moisture is adequate. Moisture conditions below the "step" are more favorable than on the general slope because snow tends to accumulate and runoff is retarded. As the "step" widens, unites with other steps, and becomes deeper as erosion extends up the slope the area of little bluestem may enlarge until it occupies most of a hillside. Little bluestem is also one of the first invaders in gulleys started by cattle trails and road ruts, and from these vantage places may spread with the course of erosion over a slope. Once established, the cover of little bluestem usually protects the slopes from excessive runoff and erosion. Since livestock ordinarily do not graze this grass the old leaves and stems accumulate on the surface. During drought periods, there is less growth and the livestock may become forced to graze it closely. The cover is thus reduced and runoff and erosion may become greatly accelerated. Grasshoppers aid in the denuding process because they also, are forced to feed on little bluestem during severe droughts.

The little bluestem type is of great ecological importance because it stabilizes areas subject to heavy runoff and erosion (see Fig. 1), holds drifting snow, hastens soil development because of the numerous roots to 3.5 feet in depth and large volume of herbage. In places little bluestem appears to be rather short-lived and to be succeeded on more moderate slopes by blue grama, western wheatgrass, needlegrass, and sedges.

The frequency-abundance analysis of the vegetation showed that *Andropogon scoparius*, with an F x A index figure of 100, was the chief dominant. In restricted places other grasses or sedges were important enough, perhaps, to rate as local dominants. The most abundant of these were *Bouteloua curtipendula*, *Koeleria cristata*, *Carex filifolia*, *C. stenophylla*, *C. pennsylvanica*, *Bouteloua gracilis*, and *Calamovilfa longifolia*. Characteristic forbs were *Echinacea angustifolia*, *Gaura coccinea*, *Helianthus rigidus*, *Senecio columbianus*, *Lygodesmia juncea*, *Calochortus nuttallii*, *Meriolix serrulata*, *Linum lewisii*, *Asclepias verticillata*, *Anemone cylindrica*, *Campanula rotundifolia*, *Heuchera hispida*, *Comandra pallida*, *Arabis holboellii*, *Drymocalis arguta*, and *Solidago* spp.

Characteristics of the little bluestem type are:

1) Dominant: *Andropogon scoparius.*
2) Topography: fairly steep slopes.
3) High total number of species per area, averaging about 50, of which about one-third are grasses.
4) The soil texture varied greatly in different horizons, ranging from sandy loam to silty clay. Most of the horizons were clay loam, silt loam, or loam.
5) The layer of dark soil was shallow, 1.5 to 7 inches.

6) Moisture-holding capacity of the soil was moderately high, 52 to 68 percent.
7) Loss-on-ignition was low, 2 to 8 percent.
8) Effervescence with HCl began on the surface.
9) Soil was usually alkaline throughout, pH 7.2 to 8.4.
10) Carbonate content was high, usually 20 to 30 percent.
11) Soil colloids high, 20 to 50 percent.
12) Total soluble salts moderately low, 312 to 743 p.p.m.
13) Calcium medium high to high, potassium and phosphorus low, sodium and chlorine negligible.
14) Profile not well developed.

4. *Sandgrass type* (Fig. 8). Test areas 21, 22, 23, and 24 have been classified in this type which is found widely on sandy ridges and hills in this region. The soil is apparently residual in origin. Both vegetation and soil are in moderately early stages of development. The high water absorbing capacity of the soil and the dense, tall growth of sandgrass prevent excessive runoff or erosion. Since Calamovilfa is no palatable to livestock and therefore usually not grazed it is not damaged in pastures. Plowing or excessive trampling may lead to wind erosion.

The average frequency-abundance of the most important grasses and sedges in this type shows *Calamovilfa longifolia* 59 (40-84), *Carex filifolia* 49 (16-84), *C. stenophylla* and *C. pennsylvanica* 58 (1-90), *Stipa comata* 35 (26-44), *Bouteloua gracilis* 29 (13-47), *Koeleria cristata* 17 (10-25), and *Andropogon scoparius* 9 (0-18). Although several of these species have high F x A index figures, Calamovilfa is the only one rated as a dominant because of its much greater height, deeply penetrating and numerous roots, and general vigor. This type is apparently developing into the first type, grama-needlegrass-sedge type. Calamovilfa is in control but factors are operating which are more favorable for growth of the secondary grasses than for Calamovilfa. Some of these factors are the shallow penetration of rainfall during the recent successive droughts, reduced height growth of Calamovilfa permitting more light to enter and the reactions of Calamovilfa roots upon soil development.

The F x A index figure for forbs was low in this type, averaging 12.5 (7-16). Some of the more common forbs were *Lygodesmia juncea, Psoralea argophylla, Aster multiflorus, Liatris punctata, Artemisia gnaphalodes, A. frigida, Asclepias verticillata, Phlox hoodii, Echinacea angustifolia, Chrysopsis villosa, Lithospermum linearifolium, Lesquerella arenosa*, and *Chenopodium leptophyllum*. This list resembles the one of forbs for the first type.

Characteristics of the sandgrass type are:

1) Dominant: *Calamovilfa longifolia*. Important secondary species; *Carex filifolia, C. stenophylla, C. pennsylvanica, Bouteloua gracilis, Stipa comata*, and *Koeleria cristata*.
2) Topography: Sandy ridges and hills, apparently residual in origin.

3) Moderately high total number of species (35 to 42), about two-thirds of which are forbs.
4) The soil texture is a highly uniform sandy loam, the sand content to depths of 5 and 6 feet averaging about 73 percent (60-87).
5) The depth to which the dark soil extended varied considerably, from 0 to 19 inches.
6) Moisture-holding capacity of the soil was moderately low, ranging from 41 to 53 percent.
7) Loss-on-ignition was very low, 2 to 4 percent.
8) The depth at which effervescence with HCl began varied greatly, from the surface in area 21 to below 72 inches in area 24.
9) Except in area 21 the soil showed acid reaction (pH 6.11-6.85) to depths varying from 39 to 69 inches. The rest of the soil varied from pH 7.04 to 7.70.
10) Carbonate contents were low in areas 22 and 23 (4.2 to 7.5 percent) but high in area 21 (15.2 to 16.1 percent).
11) Soil colloids were low, especially in area 21 (5.1 to 10.9 percent). The maximum amount was attained in area 23 with 23.4 percent.
12) Total soluble salts were low 252 to 588 p.p.m.
13) Calcium in the soil varied from low to high, potassium and phosphorus were usually low, sodium and chlorine showed only traces in some horizons.
14) Profile not well developed.

5. *Sagebrush type* (Fig. 7). In this type are included areas 18, 19, and 20. This type is widespread in the region occurring on flats along streams and in valleys. Best developed examples of the type were found usually on flats along the Little Missouri River and along creeks with permanent water as Garner Creek. This type is subject to flooding, erosion, and deposition due to storm waters which overflow the narrow stream channels. Stratification and heterogeneity are conspicuous in the profiles of this recently deposited, alluvial material.

The type is characterized chiefly by the gray-colored shrub, *Artemisia cana*, growing in dense or open stands. Most commonly it grows from 3 to 4 feet tall. Usually there is considerable grass growing in and between the bushes. While sagebrush, because of its abundance and height growth, is the major dominant, several grasses, *Agropyron smithii, Bouteloua gracilis,* and *Stipa viridula,* are of sufficient abundance and influence to rank as dominants but of less importance. The frequency-abundance of *Artemisia cana* averaged 48 (24-90), *Agropyron smithii* 88 (67-100), *Bouteloua gracilis* 41 (0-75), and *Stipa viridula* 34 (4-50). These index figures, which register only frequency and abundance, do not tell the complete story regarding dominance because the taller growth and greater volume of sagebrush are not incuded. Other species of grasses or sedges were very low in both frequency and abundance, appearing as accidental.

Forbs were usually not abundant in this type, the F x A index figure averaging 10 (5-19). The chief forbs, all with very low F x A indices, were: *Vicia sparsifolia, Lappula occidentalis, Musineon divaricatum, Malvastrum*

coccineum, Plantago purshii, Chenopodium leptophyllum, Linum rigidum, Lepidium densiflorum, and *Allium reticulatum.*

The absence of *Bouteloua gracilis*, the much lower frequency and abundance of *Stipa viridula,* and the higher frequency and abundance in area 19 as compared with areas 18 and 20 appear to be due to the greater amount of recent deposition of soil material in area 19. The stream channel is more shallow, the valley is narrower, and the laminations are much plainer in area 19. There were numerous other evidences of frequent flooding and deposition over area 19, as small gulleys, moist deposits, and débris in the branches of sagebrush. Bouteloua is not able, and Stipa has difficulty, to grow under these unstable conditions; but *Agropyron smithii,* with its extensive rhizomes, and Artemisia appear to thrive.

Characteristics of the sagebrush type are:

1) Chief dominant: *Artemisia cana.* Less important dominants: *Agropyron smithii, Bouteloua gracilis, Stipa viridula.*
2) Topography: Flats along streams and in valleys.
3) Total number of species was variable, 23 to 50, of which 75 to 80 percent are forbs.
4) Soil texture was variable in each horizon. Clay loam and clay were found more often than sandy loam, loam, or silt loam. The sand content reached as high as 78 percent in one horizon while in another horizon of the same profile the clay content was 58.6 percent.
5) The depth to which the dark soil had developed varied from none in area 19 to 10 and 11 inches in areas 18 and 20.
6) Water-holding capacity varied from low to high, 40 to 72 percent.
7) Loss-on-ignition varied from low to high, 2.4 to 13.4 percent.
8) Effervescence with HCl occurred in all horizons beginning at the surface.
9) Soil reaction was alkaline throughout, varying from pH 7.3 to 8.2.
10) Carbonate contents were moderately high ranging from 9.7 to 16 percent.
11) Soil colloidal content was variable, the weighted averages to the working depth ranged from 36 to 49 percent.
12) The amounts of total soluble salts were moderate, 537 to 1,220 p.p.m.
13) Calcium varied from low to high, potassium and phosphorus were usually low, in most horizons sodium was negligible but occasionally horizons with moderate amounts occurred, chlorine was negligible.
14) Profile usually not well developed.

6. *Saltgrass-western wheatgrass type* (Fig. 6). Areas 15 and 17 were classified in this type. These areas occurred on terraces 6 to 10 feet above intermittent or flowing streams. This type is subject to flooding, deposition, and erosion when the sod is broken. The stratified horizons show recent alluvial origin. Scattered young sagebrush, occurring in some areas, indicate that the course of succession may be into the sagebrush type, due possibly to improved drainage.

Agropyron smithii, F x A 46 and 100, and *Distichlis stricta,* F x A 46 and 88, were the chief dominants. *Bouteloua gracilis,* F x A 15 and 100,

was a less important dominant. *Stipa comata, Carex filifolia, Stipa viridula,* and a few other grasses were scarce.

Forbs were variable and low in F x A, 2 and 22, represented chiefly by ruderals as *Helianthus petiolaris, Iva xanthifolia, Plantago purshii,* and *Lepidium densiflorum.* Some additional species were characteristic but scarce as *Atriplex argentea, A. nuttallii, Chenopodium leptophyllum,* and *Musineon divaricatum.*

The greater frequency and abundance of Agropyron, Distichlis, and Bouteloua in area 17, as compared to area 15, were probably due to higher soil moisture throughout the season in 17. The creek bordering 17 (Fig. 6) has water in it throughout the year but in 15 the stream is usually dry.

Area 14 (Fig. 5) was similar to areas 15 and 17 but *Bouteloua gracilis* and *Stipa comata* were additional major dominants, making 4 in all. *Carex filifolia* and *Calamagrostis montanensis* were also present in 14 but not in 15 and 17. Frequency and abundance of forbs were greater also. This area was intermediate between types 1, 2, and 6. The terrace was higher above the stream than in areas 15 and 17. The soil profile was more fully developed, it was much less subject to flooding and the soil was more sandy.

Characteristics of the saltgrass-western wheatgrass type are:

1) Chief dominants: *Distichlis stricta, Agropyron smithii.* Less important dominant, *Bouteloua gracilis.*
2) Topography: Moderately low stream terraces subject to occasional flooding.
3) Total number of species was moderate, 28 to 36, three-fourths to four-fifths being forbs.
4) Soil texture was usually silt loam, varying from 26 to 40 percent sand in area 15, to 38 to 57 in area 17.
5) The layer of dark soil was shallow to moderate, 6 to 12 inches.
6) Water-holding capacity varied from moderate to high, 44 to 87 percent.
7) Loss-on-ignition varied from low to moderately high, 4 to 12 percent.
8) Effervescence with HCl began at the surface.
9) Soil reaction was mildly alkaline, pH 7.2 to 8.3.
10) Carbonate contents were moderately high, 12 to 20 percent.
11) Soil colloid contents were moderately high, 20 to 30 percent.
12) The amounts of total soluble salts varied from moderately low to high, 603 to 7,200 p.p.m.
13) Calcium was medium to high, potassium trace to extra high, sodium varied from low to high below 20 inches, chlorine was negligible.
14) Profile poorly developed.

7. Saltgrass-alkali meadow grass type. Areas 16 and 35 (Fig. 11) are classified in this type which occurs on low stream terraces and other depressions in which drainage is poor. This type is subject to fairly frequent flooding, deposition, and erosion when the sod is broken. Stratification, indicating recent alluvial origin, was pronounced in area 16, but in area 35 columnar and prismatic structure occurred. The soil in area 35 is solonetz (Kellogg 1934).

The chief dominants were *Distichlis stricta* and *Puccinellia nuttalliana*. *Agropyron smithii* and *Hordeum jubatum* were abundant on some areas. Forbs were low in frequency and abundance. The most characteristic were *Dondia depressa*, *Grindelia squarrosa*, *Atriplex argentea*, *Plantago elongata*, *Chenopodium leptophyllum*, and *Lepidium densiflorum*, and *Opuntia fragilis* which was limited to area 35.

The greater abundance of *Agropyron smithii* and *Opuntia fragilis* on area 35 than on area 16 may be due to the greater age of the first area, thus giving more opportunity for these species to invade. The soil is usually saturated with water for a longer time each year in area 16 than in area 35.

Characteristics of saltgrass-alkali meadow grass type are:

1) Chief dominants: *Distichlis stricta*, *Puccinellia nuttalliana*. In some areas *Agropyron smithii* may be a lesser dominant.
2) Topography: Low stream terraces and depressions, drainage poor.
3) Total number of species was low, 24 in area 16, of which 19 were forbs.
4) Soil texture varied from loam to clay in the different horizons. Clay content in area 16 varied from 17 to 30 percent; in area 35, 9 to 56 percent.
5) The surface soil was grayish-brown.
6) Water-holding capacity was high, 55 to 63 percent. The soil samples from the upper 4 horizons, to 14 inches, in area 35 did not absorb water when the Hilgard pans were set in water for a long time.
7) Loss-on-ignition was low, 2.6 to 7 percent.
8) Effervescence with HCl began on the surface in area 16, at 4 inches deep in area 35.
9) Soil reaction was alkaline throughout except in the surface 1.5-inch layer in area 35 where it was mildly acid, pH 6.8. Most of the soil showed moderately high alkalinity, from pH 7.7 to 8.6.
10) Carbonate contents were moderately high in area 16 (18-21 percent), low in area 35 (5-11 percent).
11) Soil colloidal content was variable and usually high, 16 to 67 percent.
12) Soluble salt contents were usually very high, reaching 11,100 p.p.m. in the 4.5-15.5-inch layer in area 16 and 13,900 p.p.m. in the 8-14-inch layer in area 35. The top 1.5-inch layer in area 35 was low (354 p.p.m.).
13) Calcium was high in 16, low to medium in 35; phosphorus reached medium to high; potassium was extra high in the upper 19 inches of 35, but only traces in 16; sodium was medium in 16, extra high in 35; chlorine was negligible.
14) Profile poorly developed.

8. *Buffalograss type*. Only one area, 33, is included in this type. Buffalograss usually grows in small patches on the lower portions of some slopes, in small draws and depressions in some valleys, and on portions of scabby, gentle slopes or flats where the soil has a high clay content. In places it plays a part in the succession following solonization and solodization (Kellogg 1934); in other places its occurrence appears to be due to overgrazing, erosion, or other disturbances.

Characteristics of the buffalograss type are:

1) Dominant: *Buchloe dactyloides,* other species scarce.
2) Topography: See above.
3) Low total number of species.
4) Soil texture; usually clay, in area 33 most horizons had 37 percent or more clay.
5) Surface layer of dark soil 7 inches deep in area 33.
6) Water-holding capacity high, in area 33 usually 57 to 60 percent.
7) Loss-on-ignition moderately low, 3 to 6 percent.
8) Effervescence with HC1 close to surface, at 7 inches in area 33.
9) Soil reaction mildly alkaline, pH 7.4-7.8.
10) Low carbonate content, 6.3-9.5 percent.
11) Soil colloids high, usually 45 to 62 percent in area 33.
12) Total soluble salts were usually high, mostly 1002 to 2456 p.p.m. in area 33.
13) Calcium low to medium high, potassium, phosphorus, sodium, and chlorine negligible to low.
14) Profile moderately well developed.

9. *Big bluestem type* (Fig. 4). Areas 27, 28, 29, and 32 were classified in this type. The small areas of this type were usually located on the lower parts of steep slopes, as in narrow valleys and draws. The type is important because it represents the best developed grassland in the region and it is unexcelled for summer grazing. This type, evidently, requires more moisture than that furnished only by direct precipitation. The additional moisture is received by runoff from slopes above and possibly from melting snow drifts and seepage. Vegetation and soil showed maximum development in this region, more typical of the true prairie in eastern North Dakota. The small areas of this type in this region, then, are minute outliers of the true prairie.

The F x A index figure of *Andropogon furcatus,* the dominant, ranged from 95 to 100. Other important grasses were *Andropogon scoparius* (33-95), *Koeleria cristata* (1-12), *Bouteloua curtipendula* (1-22), *Carex stenophylla* (0-53), and *C. pennsylvanica* (0-51).

The frequency and abundance of forbs were high, F x A ranging from 24 to 41 percent. The most numerous were *Astragalus hypoglottis, Helianthus rigidus, Echinacea angustifolia, Campanula rotundifolia, Cerastium arvense, Anemone cylindrica,* and *Psoralea argophylla. Rosa suffulta* and *Symphoricarpos occidentalis* occurred frequently due to more favorable soil moisture conditions. Area 28 had a greater number of species, greater frequency-abundance of forbs and of more mesophytic grasses as *Stipa spartea* and *Elymus glaucus* and less *Andropogon scoparius* and *Bouteloua curtipendula* than areas 27, 29, and 32.

Area 30 (Fig. 9) may be considered as an example of the highest mesophytic development of the big bluestem type, found only where soil moisture is especially suitable. *Sporobolus heterolepsis* was dominant with *Andropogon furcatus.* Other prairie species in greater abundance or restricted to this area were *Panicum virgatum, Elymus glaucus, Stipa spartea, Agropyron tenerum, Juncus balticus, Carex pennsylvanica, Avena hookeri,*

Lilium umbellatum, Helianthus subrhomboideus, H. maximilliana, Liatris scariosa, and *Glycyrrhiza lepidota.* There was a total of 86 species in this area, averaging 20.3 species per m² quadrat.

Characteristics of the big bluestem type are:

1) Dominant: *Andropogon furcatus.* On dry portions *A. scoparius* is a less important dominant, on moist areas *Sporobolus heterolepis* is also dominant.
2) Topography: Lower parts of slopes where moisture in addition to direct precipitation is received.
3) High total number of species, 41 to 63, three-fourths to four-fifths being forbs.
4) Soil texture, loam to sandy loam, usually 40 to 55 percent sand.
5) Layer of dark soil usually deep. In area 28, however, it was only 9 inches deep, in the others 15 to 46 inches.
6) Water-holding capacity was high, especially in the surface 4 to 6-inch layer where it was usually 90 percent or more. Below this it varied from about 50 to 75 percent.
7) Loss-on-ignition was high in the surface 4 to 6 inches, 10 to 13 percent; low to moderate below, 4 to 9 percent.
8) The depth at which effervescence with HCl began, varied from 4 to 25 inches, 33 inches in area 30.
9) Soil reaction was usually acid to depths of 20 to 32 inches. In area 28, the pH was as low as 5.5 in the surface 4 inches.
10) Carbonate contents varied considerably, from 5 to 27 percent.
11) Soil colloids varied from low to high, but usually ranged from 18 to 35 percent. They were noticeably lower in area 30, 8 to 17 percent.
12) Total soluble salts were low, 329 to 678 p.p.m.
13) Calcium content was usually medium, potassium was usually low, but in area 30 it was extra high to depth of 18 inches.
14) Profile well developed.

Miscellaneous areas. Numbers 5, 8, and 9, located on gradually sloping higher stream terraces were intermediate between types 1 and 2. The dominants on these areas were *Bouteloua gracilis, Agropyron smithii, Stipa comata,* and *Carex* spp. *Koeleria cristata* also occurred on each of these areas. The representation of forbs was similar to types 1 and 2. The total number of species varied from 18 to 42. Soil characteristics were usually intermediate between the two types as soil texture which was clay loam, depth of dark soil 7 to 10 inches, effervescence began at 7 to 10 inches and surface soil mildly acid or alkaline. It appears that soil and vegetation on these areas were transitional in development from the western wheatgrass-grama-sedge type to the grama-needlegrass type.

Area 34 (see Fig. 10) was the only locality found that showed dominance of *Bouteloua gracilis* and *Poa buckleyana.* Other species were *Malvastrum coccineum, Plantago purshii, Artemisia dracunculoides, Agropyron smithii, Stipa viridula, S. comata* and a few additional forbs. The soil contained an unusually high percentage of clay and silt averaging 73 to the

working depth, and the hard columnar structure indicated that this may have been a solonetz soil.[1]

DISCUSSION

Classification of vegetation in western North Dakota is difficult because of the great heterogeneity due to variations in topography, soil conditions, wind and water erosion, water penetration, and to the various kinds of succession and stages in succession (see Figs. 1, 5). Seres are occurring on recently eroded banks, on recent depositions, on saline depressions, on sandy hills and ridges, on abandoned cultivated lands, and on areas depleted by grasshoppers, drought, and overgrazing. Since successional sequences have not yet been determined it is not possibe to make a classification which will show relationship between the different types. The importance of succession in the tall-grass prairie has been discussed by Weaver and Fitzpatrick (1934, pp. 281-288).

In the Little Missouri country it appears that the grama-needlegrass-sedge type (Figs. 2, 3) on upland plateaus and gentle upland slopes is nearer stabilization with climatic conditions than any of the other types studied. This type has had the longest period of time in which to reach stabilization. The western wheatgrass-grama-sedge type (Fig. 4) appears to be a successional stage on slopes developing in the direction of the first type. Areas 5, 8, and 9 appear to be further along in this succession than the western wheatgrass-grama-sedge areas. The big bluestem type is a more mesophytic type than the grama-needlegrass-sedge type but it cannot be considered climatically stabilized because it is located in places where moisture in excess of direct precipitation is received (Fig. 4). It does not seem possible that direct precipitation in this region can support this true prairie type (Fig. 11). The little bluestem type appears to be a successional stage following erosion on many slopes (Fig. 4). The sandgrass type is a successional stage on sandy areas (Fig. 8). The sagebrush type (Fig. 7) appears to be a successional stage on terraces where soil moisture is usually available in the subsoil throughout the season. As the stream erodes a deeper channel, and the terrace becomes drier, types 2 or 1 may replace the sagebrush type. The saltgrass-western wheatgrass and the saltgrass-alkali meadow grass types belong in a halosere on poorly drained or solonetz soils (Fig. 11). Buffalograss communities occur in secondary seres following cultivation, overgrazing, and salinization. The course of plant succession in relation to soil characteristics and development requires long-continued investigations on areas reserved for this purpose. (Tansley 1935; Shelford and Hanson 1936).

Other types, not treated in this paper, occur in the region, as the shrub types in valleys (Symphoricarpos, Rosa, Ribes, Prunus), the *Pinus ponderosa* type near Ranger, the Juniperus type, the Fraxinus-Acer type in

[1] Because of the acid reaction in the leached portion of the profile above the columns, Dr. Charles E. Kellogg, Chief, Division Soil Survey, U. S. Bureau of Chemistry and Soils, suggests that it would be more accurate to say "solodized solonetz" rather than "solonetz." (See profile description).

draws, and the *Populus deltoides* type on the Little Missouri River floodplain (see Figs. 1, 5). The early successional stages following erosion, deposition, and cultivation, have not been discussed, but all the major grassland types are included.

The problem of the relation of vegetation and the soil is one of exceeding complexity. The soil and the vegetation are both dynamic unities developed and controlled largely by the environmental forces acting upon them. Soil science has stressed the importance of native vegetation in the development of the soil. Ecological studies have shown the important influence of the soil on the development and structure of native vegetation.

Observation has shown that some plants grow better on certain soils than on others, and that certain native plants indicate soils suitable for raising some kinds of crops while other native plants indicate that the soil is unsuitable for the same crops. Considerable study has been devoted to the relation of forest cover to soil conditions but the relation of grassland to soil has not been investigated to nearly as great an extent.

Clements (1920) has summarized the earlier work on the relation of vegetation type to soil type. Kearney, Briggs, Shantz, McLane, and Piemeisel (1914) studied the vegetation of the Tooele Valley, Utah, with the object of determining and correlating the distribution of the vegetation with the physical and chemical properties of the soil. They found relationships between moisture content, soil texture, alkali salts, and vegetation.

Aldous and Shantz (1924) distinguished over 100 vegetation types in the arid and semiarid portions of the United States and evaluated them as to grazing and agricultural use. Shantz and Piemeisel (1924) distinguished vegetation types characteristic of certain soil conditions in the southwestern desert region, emphasizing particularly salt content and water relations. Newton and Nowosad (1933) in Quebec studied the relation of three types of soil to the flora of open and woodland permanent pastures. Cole and Dubey (1932) described the value of permanent pastures in Romney Marsh, England, in relation to soil profile, emphasizing soil texture and drainage conditions.

Frolick and Keim (1933) found the influence of the ground water table and soil texture to be the chief factors in determining the existence of distinctive plant communities in the prairie hay district of Nebraska. Steiger (1930), also in Nebraska, found the water content of the soil the most important factor determining differences in the structure of the vegetation.

The vegetation types are principally distinguished on the basis of the dominant species in the plant association and the topographical situation (see Figs. 1, 4, 5). This linkage between topographical position and the nature of the vegetation cover is best explained on the basis that different topographical situations present different environments for the development of the vegetation and soil types. This has long been recognized by soil sur-

veyors who frequently correlate differences of soil characteristics and, hence, soil series, with situation of the soil. The topographical position of a type is often an indicator of the geologic material from which the soil has been developed and of soil moisture conditions.

A comparison of the data for the test areas of the different types shows that there is considerable difference in textural composition between the profiles of the areas within the different types, as well as between types (see Table 1). Yet in general there is a similarity in textural composition of areas within types, while there is considerable variation between types.

Textural heterogeneity between types is indicated by changes in the structure of the vegetation. The working depths of the roots in the various vegetation types furnish a fairly good index to textural differences since they represent, except where influenced by other conditions, the depth of moisture penetration. Thus in the first two types moisture penetration is about 30 inches. This is further confirmed by the tendency of these types to accumulate carbonates in a definite horizon at this approximate depth. In the sandgrass type, on the other hand, the percentage of total sands is greater and the texture is somewhat coarser, for the working depth indicates that moisture penetrates on the average about twice as far as in the first type.

Textural differences also show their influence in another way. One of the outstanding differences between the grama-needlegrass-sedge and the western wheatgrass-grama-sedge types is in the total number of species found on each of the two types. Another difference is the much larger percentage of finer materials in the soil of the second type. The fact that a lower total number of species seems related to the higher percentage of finer material in the profile indicates the influence of texture on producing heterogeneity in vegetation. It seems likely that the effect here is an indirect one and is related to the wilting coefficient.

However, soil texture seems intimately bound up with that of soil moisture in influencing the composition of the vegetation (Frolick and Keim 1933, Steiger 1930). Metzger (1935) found that a low moisture supply tends to show soil heterogeneity, as measured by crop yields, while a high moisture supply seems to obscure it. Thorp (1931) related soil profile and precipitation to the vegetation in Wyoming.

Within a region where the precipitation is essentially the same and other climatic factors are largely similar, an increased supply of moisture in the soil will be indicated by a difference in vegetation. In general there are two sources of additional moisture, the presence of a water table, or seepage from other areas. Five of the different grassland vegetation types are produced under conditions where additional soil moisture is available. They are little bluestem, big bluestem, sagebrush, saltgrass-western wheatgrass, and saltgrass-alkali meadow grass (Figs. 4, 5, 6).

The little bluestem type and the big bluestem type apparently receive moisture by seepage from surrounding areas (Fig. 4). Their location on slopes suggests that moisture that is received on other areas by means of precipitation percolates through the soil and, meeting impervious layers, seeps out to become available to the roots of the bluestems. The profiles of these types were more moist than the profiles of grama-needlegrass-sedge, western wheatgrass-grama-sedge and sandgrass types. The moisture supply seems to be particularly favorable where the big bluestem type is developed. The flora of this type compares favorably with that of the true prairie developed under an annual rainfall of over 20 inches.

The sagebrush type and the saltgrass types (Figs. 5, 6) are developed under the influence of a water table that is within the range of the roots at least for a part of the season. The water table is generally deeper under the sagebrush type than it is under the saltgrass types. In the latter the presence of a water table close to the surface may be a limiting factor in root growth. This is indicated by the relatively shallow working depth of the roots. The high content of alkali salts is also an important factor influencing the development of the vegetation and soil of the saltgrass types (Table 1).

Kelley (1922, 1923) found that soil acidity influences the flora to a considerable extent, although he concludes that it is possibly never the single controlling factor in plant growth. Geisler (1926) found nothing to indicate that soil reactions are responsible for species distribution in the Cincinnati region. Young (1934) found a certain relationship between soil reaction and plant distribution, particularly in regard to the high acidity of certain soil types.

The soil reactions of most of the types studied in this investigation were alkaline. Only in the grama-needlegrass-sedge, sandgrass and big bluestem types was there significant acidity, and in these types the general range of reaction of the surface horizons was usually mildly acid. While this may have some bearing on the nature of the vegetation, the effect seems slight in comparison with the influence of the factors of moisture, soil texture, and soluble salts.

In the grama-needlegrass-sedge type the acidity of the surface horizons seems to indicate the relative age and maturity of this type as compared with the others. To quote Marbut (1928, p. 192): "It seems to be possible for the solution to become acid in that part of the zone where the amount of moisture available is still too small to prevent the zone of carbonate accumulation in part of the solum, but is large enough to finally remove the bases from the upper part of the solum and produce an acid soil. . . . but if the local environment were to remain unchanged through earth crustal movements, or by any other processes, long enough, it is apparent that the surface may possibly become acid." The acidity of the surface of some areas of the sandgrass type and the big bluestem type is suggestive of leaching, in the first case

influenced by the coarser texture of the material and in the second case by the excess moisture supply.

In addition to the factors examined in this study there are many others that should be investigated. Kellogg (1930) has emphasized the importance of base exchange in relation to plant growth. Jenny (1935) has correlated the units of base exchange material present in the soil with the growth of bluegrass in Missouri grasslands. The relation of organic matter and nitrogen content to soil texture is important, as has been pointed out by Russel and McRuer (1927). Definite soil moisture readings taken at different times during the season in the different types would be of great value.

SUMMARY

1. Characteristics of 36 areas of grassland in the Little Missouri region of western North Dakota were studied, chiefly during the summer of 1935. These 36 areas were classified in 9 vegetation types.

2. The 9 major types were 1) grama-needlegrass-sedge, 2) western wheatgrass-grama-sedge, 3) little bluestem, 4) sandgrass, 5) sagebrush, 6) saltgrass-western wheatgrass, 7) saltgrass-alkali meadow grass, 8) buffalograss, 9) big bluestem.

3. Botanical analyses of the vegetation were made by the frequency-abundance and point methods. Soil profiles were described in the field and soil samples from the various horizons were analyzed in the laboratory for chemical and physical characteristics. The characteristics of each type are summarized under "Classification of Test Areas into Types."

4. The 9 types differed chiefly in botanical composition, topographic location, thickness of surface layer of dark soil, depth at which effervescence with HCl began, acidity or alkalinity of the surface horizons, total concentration of soluble salts, sodium and carbonate contents, soil texture, and colloidal content.

5. The results show a definite relationship between soil heterogeneity and vegetation heterogeneity. There are distinctive soil differences and vegetation differences between the types. The mechanical analyses of the soils indicate heterogeneity in textural types which corresponds, in a measure, to the heterogeneity in grassland vegetation types but it is not assumed that textural differences are chiefly responsible for vegetational differences. Topographical position is important because different topographical situations present different environments for the development of vegetation and soil types. Although the exact role of each influencing factor has not been determined the duration of available soil moisture, depth to the water table, concentration of salts, and stage in various successional seres, are all important in determining vegetation types in this region.

6. The grama-needlegrass-sedge type appeared to have reached the highest degree of stabilization in relation to the climate, and the soil of this type

most nearly approaches the typical profile of the dark brown soils. The big bluestem type appeared to depend upon moisture additional to that received by precipitation. The other types appeared to be successional stages following erosion, deposition, salinization, overgrazing, or cultivation.

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THE EFFECT OF VEGETATION ON THE GROWTH OF LONGLEAF PINE SEEDLINGS

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[1] Former field assistants Lincoln Ellison and Allan G. Watkins rendered valuable assistance in the installation of the plots and in some of the subsequent field work.

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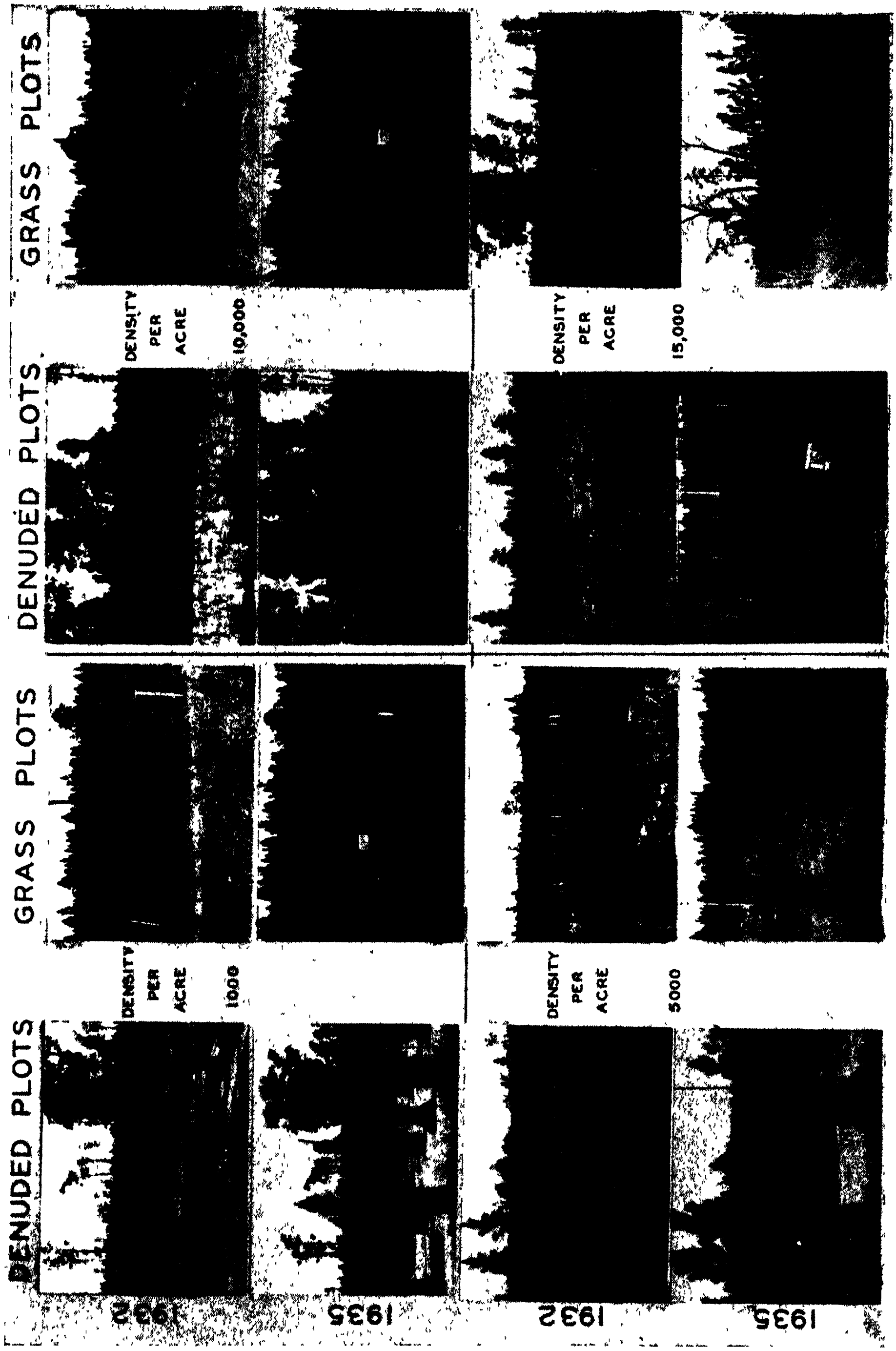
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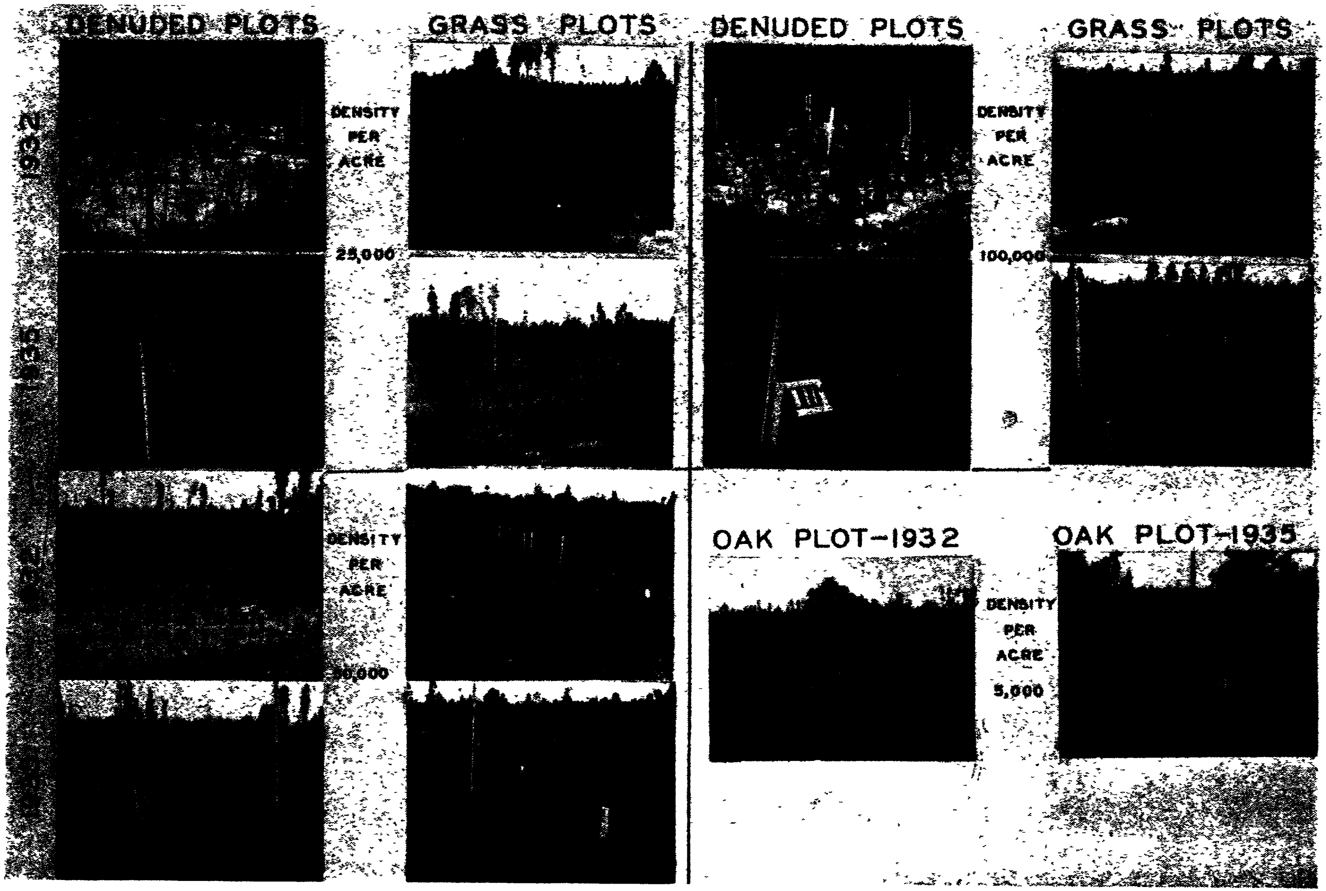
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THE EFFECT OF VEGETATION ON THE GROWTH OF LONGLEAF PINE SEEDLINGS

INTRODUCTION

Seedlings of longleaf pine (*Pinus palustris* Miller) growing under natural conditions exhibit characteristics which are not found among the other species of southern pines. The seeds of this pine germinate in autumn and by spring the seedlings generally have already shed their cotyledons. Also unlike the seedlings of other pines, those of longleaf pine develop a carrot-like taproot during early life and seem to endure a variety of site conditions. The greatest difference between longleaf pine seedlings and those of the other pines, however, is in the slow growth of the stem during the first few years. Even 4 or 5 years (and often longer) after germination the stem is hardly visible above ground, and the long leaves are often indistinguishable from the surrounding grasses (Fig. 1).

FIG. 1. Typical longleaf pine seedlings growing under natural conditions. At the right is a 7-year-old and at the left a 4-year-old seedling.

Not only do longleaf pine seedlings differ from other pine seedlings in the rate of growth of their stems, but they also differ among themselves. It is not uncommon to find longleaf pine seedlings 8 years old having a stem height of but 3 centimeters (1.18 inches), while other seedlings of the same species only half that age may be four times as tall. Various explanations have been offered for such differences in growth. The site is frequently regarded as the cause of the growth differences. Sometimes annual fires are blamed for the retardation in growth of the seedlings. Recently Siggers (1932) has shown that the brown-spot leaf blight (*Septoria acicola* (Thüm.) Sacc.) definitely retards the growth of longleaf pine seedlings through causing premature defoliation. Obviously all these factors may operate in nature,

either singly or in combinations, and the degree of the effect on the growth of the pines depends on the intensity of the factors.

Root competition is another factor that has sometimes been mentioned as the cause of the slow growth of longleaf pine seedlings, but the effect of this factor has been observed mostly in the field. It was the object of this study to determine definitely whether the vegetation commonly associated with pine seedlings affects their growth. Inasmuch as the vegetation is composed of grasses, herbs, scrub oaks, and pine seedlings, the study was divided into three parts: (1) the effect of the ground cover (grasses and herbs) on the growth of pine seedlings; (2) the effect of the number of seedlings occupying a definite area (density of stocking) on the rate of growth of their stems; and (3) the effect of the ground cover together with scrub oaks on the rate of growth of the pine seedlings growing in that area.

RESUMÉ OF LITERATURE ON COMPETITION

Competition among plants was first suggested by Petrus de Crescentiis as early as 1305. Later, Buffon (1745), Duhamel du Monceau (1760), Varenne de Fenille (1790), De Candolle (1820), Darwin (1859), and Nageli (1874) all made reference to the same subject. In 1904 Fricke challenged the commonly accepted idea of his day that competition among plants was mainly for light, and stated that competition for moisture among the roots of plants was even more important. He arrived at this conclusion by surrounding a stand of *Pinus silvestris* Linn. with a trench, severing the roots of adjacent plants, and freeing the plants in the enclosed area from competing roots. He found that in this area the young suppressed trees showed a marked increase in growth, and that the ground cover changed to a luxuriant stand, including species not found outside of the trenched area. He also sowed seed of pine, spruce, and oak in areas, which he surrounded with a trench. Here again not only was there an increase in growth of the seedlings, but also the germination was much better than in areas that had not been trenched. The moisture content of the soil in the trenched area was two to three times as great as in the untrenched areas.

Clements in the same year (1904) pointed out that competition was keener between species of like form than between those of dissimilar form and that the degree of competition increased as the density of the stand increased. Working with seedlings of *Pinus contorta* Loudon, Clements (1910) found that competition among the pine seedlings for water was very keen whenever their roots entered the same area, and particularly when the water content was relatively low. Competition for light, however, did not begin until height growth of the seedlings was well under way.

According to Sherff (1912), two or more species may live together without competing with each other if their roots lie at different depths, or

even if the roots lie in the same depths, if their demands on the soil are unlike. This was later confirmed by Salisbury (1924).

Aaltonen (1923) regarded light as a subordinate factor in the forest and emphasized the fact that the struggle for room is influenced by the subterranean rather than by the aerial parts of a tree. In a later paper (1926), he considered the lack of seedlings near old trees as due to competition for water and mineral foods and he reiterated his earlier statement that the space arrangement of the aerial parts of trees was decided by their roots and the competition existing between them in the ground, thus substantiating the views of earlier workers, Cotta, Borggreve, and Fricke. Aaltonen held the competition among even-aged trees to be even more important than that between seedlings and the mother tree.

Pearson (1923) found that bunch grasses in the Southwest retard the development of *Pinus ponderosa* Lawson seedlings. He attributed this retardation mainly to root competition. Yapp (1925) regarded competition as the chief factor in the establishment of a plant community, and Burns (1927) found that leaf development was influenced principally by the water content of the substratum and that the amount of water in the soil affected the density of the crown more so than did the light.

Fabricius (1927) laid out a trenched and an untrenched plot under a mature, well-closed spruce stand and found that on the trenched plot the seedlings were dark green and apparently more vigorous than those on the untrenched plot. On the trenched plot the annual growth in height of the seedlings was nearly six times that of the seedlings on the check plot. In a later paper (1930), he showed that a deficiency of water and a deficiency of light produced by the old stand each caused a distinct retarding of the growth of the seedlings under the canopy, and he concluded that root competition played a very important rôle in the growth of seedlings in a stand of older trees. In fact, where light was sufficient, root competition acted as the limiting factor.

According to Clements, Weaver, and Hanson (1929), competition among plants begins when the immediate supply of a single necessary factor falls below the combined demands of the plants. Competition, they claim, is a combined need in excess of the supply. It exists only where two or more individuals together seek more than is afforded by the space they occupy. Plants, they state, compete mainly for light, water, and nutrients, water being most important and nutrients least.

Toumey and Kienholz (1929) found that during the driest part of the year there was two to nine times as much moisture in the upper 6 inches of the soil in a plot surrounded by a trench as in that of an untrenched plot. They attributed this difference wholly to the elimination of root competition in the trenched plot. When the soil moisture was abundant, trenching exerted little influence on the amount of available moisture present in the

soil. They also found that on the untrenched plot the vegetation, eight years after the establishment of the plots, remained very sparse, while the trenched plot was covered by a dense mass of vegetation; on the untrenched plot, the density of the vegetation was 8.1 percent, while on the trenched plot it was 80 percent. The hemlocks on the untrenched plots averaged 2.5 inches in height, while on the trenched plot they averaged 37.7 inches. The differences were attributed to the lack of root competition on the trenched plot, resulting in a higher moisture content of the soil. These results substantiate those obtained previously by Phillips (1928). Pearson (1930), however, claims that even though trenching may increase moisture content, an increased soil temperature is likewise necessary for ponderosa pine in Arizona.

Coster (1933) found that when a teak plantation adjoins an older crop, the trees at the edge are behind in development and some even die. Experimentation proved that this was caused by the competition of the older roots and that competition for nutrients is negligible. Coster also found that when teak is mixed with other species, the diameter increment is markedly affected. He recommends that ditches be dug around younger plantations and even in blanks where replacements are made. Mixed plantings for teak are undesirable because of the unfavorable effect of root competition on the growth of teak. He concludes that on infertile soils thick undergrowth on areas protected from fire hinders the growth of teak.

HISTORY AND DESCRIPTION OF THE EXPERIMENTAL AREA

The experimental area is located between parallels 30° 48′ and 30° 50′ North Latitude in Washington Parish, 10 miles northwest of Bogalusa, Louisiana.

The area was formerly occupied by a stand of old longleaf pine, the dominant trees of which reached a height of over 110 feet. In 1920 the area was burned over prior to seedfall and the trees were cut. The logging took place in October and November, during an unusually heavy seedfall. Because many of the tree tops were left on the ground immediately after logging, the seed, which under normal conditions would have been widely scattered, remained on the ground in dense patches. This condition resulted in a very dense stand of seedlings. When examined in 1932, 12 years after seedfall, the number of seedlings still ran from 30 to 435 to the milacre[1] and most of them were still in the "grass stage"—that is, their crowns were below or on the same level with the surrounding grass tops, making the seedlings often indistinguishable from the grass. The area itself at the time of the establishment of the experiment was sprinkled generously with scrub oaks, principally *Quercus marilandica* Muench. and *Q. stellata* Wang. Saplings of longleaf pine, presumably of the same age (12 years old) as the seedlings and more than 6 feet in height, were scattered over the area. Work was

[1] An area 6.6 feet square comprising 0.001 acre.

started on the establishment of plots on March 23, 1932. By August of that year all the plots were established and data on various environmental factors were being collected.

The area is gently rolling and about 53.3 meters (175 feet) above sea level. Washington Parish lies in the geologic formation known as the Citronelle of the Gulf Coastal Plain (Matson and Berry 1916). The original surface of this formation sloped gently towards the Gulf, but at present the surface consists of slopes interrupted by terraces. In a few places remnants of the original surface of this formation may be seen, but these are frequently covered with water. The materials of the lower plain of the Citronelle formation were laid down toward the end of the Pliocene. The soil on the experimental area is predominantly Ruston fine sandy loam, but in places there are also outcroppings of Orangeburg fine sandy loam. The entire experimental area is well drained.

The vegetation on the area was typical of the upland soils of the longleaf pine belt (Pessin 1933). Three strip transects running east to west were laid out and the vegetation on these listed in April and again in August. These strips were 40.2 m. apart and each was 20.1 m. long and 19.0 cm. wide. Following are listed the plants found on the area together with the relative proportion of the ground cover occupied by each species. The pines and the oaks are omitted from this list, since these are considered separately.

VEGETATION ON THE EXPERIMENTAL AREA

Species	*Percent of population*
Panicum aciculare Desv.	18
Andropogon scoparius Michx.	17
Andropogon elliottii Chapm.	16
Lasiococcus dumosus Small (*Gaylussacia dumosa*)	14
Helianthus radula T & G.	10
Andropogon tener Kunth.	5
Drosera brevifolia Pursh.	3
Cerothamnus ceriferus Small (*Myrica cerifera*)	3
Panicum strigosum Muhl.	3
Pityopsis graminifolia Nutt. (*Chrysopsis graminifolia*)	3
Gracca virginiana L.	2
Crotalaria purshii D. C.	2
Cyanococcus myrsinites Small (*Vaccinium myrsinites*)	1
Tithymalopsis corollata Small (*Euphorbia corollata*)	Scattered
Pinguicula lutea Walt.	"
Pilostaxis lutea Small (*Polygala lutea*)	"
Stylosanthes biflora B. S. P.	"
Viola sp.	"
Trilisa odoratissima Cass.	"
Rhynchosia simplicifolia Wood	"
Gnaphalium purpureum L.	"
Laciniaria graminifolia Kuntze	"
Elephantopus tomentosus L.	"

Hypoxis hirsuta Coville	Scattered
Smilax bona-nox L.	"
Rhus copallinum L.	"
Phlox pilosa L.	"
Sisyrinchium graminoides Bicknell	"
Pteridium aqualina Kuhn	"

The last 16 species compose about three percent of the plant population.

CLIMATE

Data collected in Franklinton, Louisiana, 11 miles west of the plots, showed that for six years (1926-32) the mean annual rainfall for this region was 61.31 inches. The mean temperature during the winter months for this period was 58.5°F.; during the spring months 64.3°F.; during the summer months 79.3°F.; and during the autumn 66.9°F. The mean annual temperature for the period between 1926 and 1932 was 67.2°F. The average date of the last killing frost was March 6 and the average date of the first killing frost was November 8. For each year there were approximately 246 frost-free days.

When the area was selected for this study a weather shelter was erected in which a Friez hygrothermograph was installed to record the relative humidity and the temperature of the atmosphere. The instrument was placed at 0.6 m. above ground. The velocity of the wind at the same height was measured by means of a 3-cup Friez anemometer, and the evaporation rate was determined by means of standardized Livingston spherical white porus clay cup atmometers equipped with mercury rain-correcting valves. The reservoir supply bottles were of 1-liter capacity. All the readings were corrected by the coefficients to the standard. At frequent intervals the cups were cleaned with alcohol to remove the algal growth which sometimes accumulated at the base of the sphere. Due to the prevalent high temperature, the necks of the cups had to be reshellacked at intervals of about six weeks. The amount of water evaporated was measured weekly and calculated on the basis of average daily evaporation. The rainfall data were measured with a standard Weather Bureau type rain gauge and the amount was recorded daily.

The temperature, relative humidity, and wind data for the experimental area for the growing seasons (April to October) of 1932, 1933, and 1934 are summarized in Table 1.

TEMPERATURE

The data indicate that the mean temperature during the growing season differed very little from year to year. In 1932 the mean temperature for the growing season was 73°F.; in 1933, 74°F.; and in 1934, 75°F. The average daily maximum temperature of 90°F. and above in 1932 occurred in July and August; in 1933 in June, August, and September; and in 1934 in June, July, and August.

WIND

The windiest months recorded during 1932 were May and September; in 1933, April, May, and July; while in 1934, May alone showed an average wind velocity of over two miles per hour.

RELATIVE HUMIDITY

In 1932 and 1934 the average daily relative humidity was lowest in April and in 1933 it was lower in June than in April.

TABLE 1. AIR TEMPERATURE, RELATIVE HUMIDITY, AND WIND VELOCITY ON THE EXPERIMENTAL AREA

Month	Mean Temperature (F)			Temperature (F)						Relative Humidity (percent)						Wind (miles per hr)		
				Ave daily max			Ave daily min			Ave daily max			Ave daily min			Ave daily velocity		
	1932	1933	1934	1932	1933	1934	1932	1933	1934	1932	1933	1934	1932	1933	1934	1932	1933	1934
April	65	64	64	81	77	76	49	51	52	81	88	80	47	56	46		2.18	
May	63	75	73	77	88	84	49	62	62	89	87	88	67	54	56	3.02	2.47	2.37
June	75	76	80	89	93	92	60	60	68	88	80	88	61	42	59	1.90	1.99	1.89
July	81	78	82	96	88	93	67	68	71	89	97	89	66	69	59	1.83	2.09	1.36
August	79	78	80	91	91	90	67	65	71	89	91	91	75	59	61	1.52	1.32	1.37
September	74	78	75	85	93	89	63	63	62	79	86	93	63	50	59	3.40	1.41	1.35
October	63	67		78	84		47	50		85	80		68	50			1.05	
Growing season	73	74	75	85	88	87	62	61	64	84	88	88	64	54	56	2.53	1.78	1.78

RAINFALL AND EVAPORATION

In Table 2 are shown the rainfall data for 1932 to 1934 and the total rainfall for each growing season. In 1933 low rainfall occurred during June, August, September, October, and November. Only 2.96 inches of rain fell from September 4 to December 4. The greatest amount of rainfall occurred between April 3 and May 15. Another wet spell occurred in July. The rainfall for March, April, May, and July constituted nearly 76 percent of the total rainfall for the year. In 1934 the distribution of the rainfall was more or less normal. July had the highest total rainfall, while March, May, and September were months with low rainfall. The total rainfall for the months of May to September for the three years was highest in 1934 and lowest in 1932.

The evaporation data (measured with Livingston porous cup atmometers) for the five months (May to September) for 1932-1934 are shown in Table 2. The average daily evaporation rate during 1932 was highest in May and lowest in August. In 1933, June had the highest average daily evaporation and May had the lowest. In 1934 the average daily evaporation did not vary much from month to month. Apparently the growing season for 1933 was the driest, and that of 1934 was the most humid. In both rainfall and evaporation the extremes were less pronounced in 1934 than in 1933.

TABLE 2. RAINFALL AND EVAPORATION

Month	Rainfall			Average Daily Evaporation		
	1932	1933	1934	1932	1933	1934
		Inches			Cubic centimeters	
January		5 49	5.81			
February		2 40	6.97			
March		11 62	3 45			
April		24.72	7 41	38 4	29 9	
May	3.43	11 93	4.25	33 9	28 6	24.2
June	3.79	1 54	6 84	31.4	43.2	29 6
July	3 58	8 56	9.78	28 2	35 7	21 1
August	6 58	1.66	7.75	21 8	31.1	26 0
September	2 58	1.88	3 44	26 6	37 4	24 2
October	3.69	0.70			46 4	
November	3 69	0.86				
December	5 71	3.68				
Total	32 97 (eight months)	75.04 (full year)	55 70 (nine months)			
Total (May-September)	19 96	25.57	32 06			
Average (May-September)				28 4	35 2	25 0

TREATMENT OF EXPERIMENTAL PLOTS

Three combinations of conditions were studied: (1) the effect of density of stocking on the rate of growth of longleaf pine seedlings; (2) the combined effect of the ground cover and density of stocking on the growth of the pine seedlings; and (3) the combined effect of the ground cover and the scrub oaks on the growth of the seedlings.

Seven plots were established in which all the oaks, herbs, and grasses were removed by hoeing, leaving on the bare ground only the selected pine seedlings, which were thinned to densities of 1, 5, 10, 15, 25, 50, and 100 seedlings per milacre. Seven more plots were laid out in which all the scrub oaks were removed, leaving only the pine seedlings and the grass and herbs; the stands of pine seedlings were thinned to the same densities as in the denuded plots. Thus, two conditions were established—in one the pine seedlings presumably competed among themselves, and in the other the pine seedlings presumably competed with each other and also with the grasses and herbs. The third condition was obtained by the establishment of one plot in which scrub oak, grasses, herbs, and pine seedlings were intermixed. This plot was left undisturbed, except for the thinning of the pine seedlings to a density of five to the milacre. The plots varied in size according to density of stocking, but 100 seedlings per plot constituted the minimum. Figure 2 shows approximately the area occupied by each pine seedling in the plots of the different densities.

During the first growing season after establishment, the denuded plots

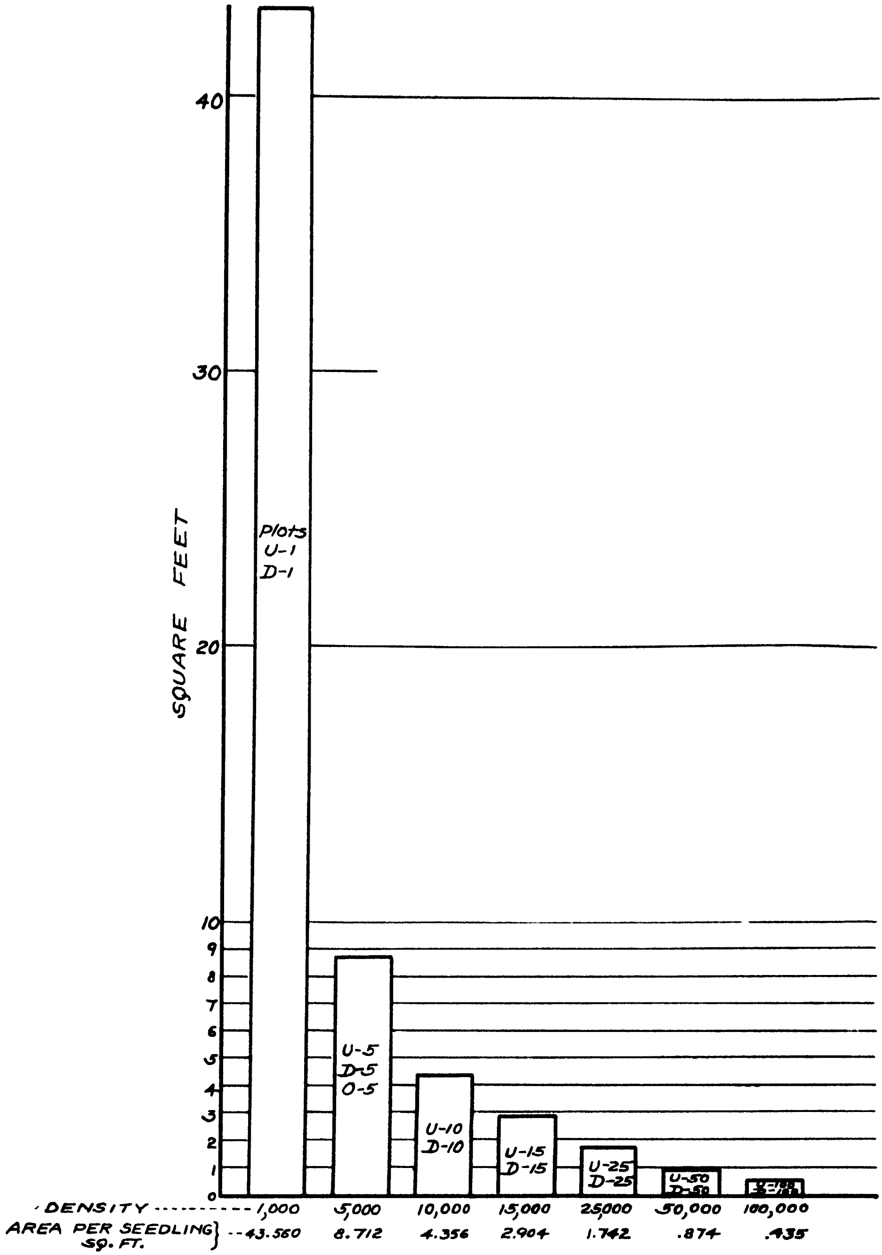

FIG. 2. Graphic presentation of surface area occupied by each pine seedling in different plots.

had to be weeded at monthly intervals, while during subsequent seasons two or three weedings per season were sufficient to keep out all weeds and grasses. The original denudation was accomplished by hoeing but after the first season only occasional herbs and grasses appeared on the denuded plots, and these were generally pulled out by hand.

In all of these plots the seedlings were selected as to uniformity of age, size, and condition of the terminal bud, and were as evenly spaced in the plots as possible. Each plot was surrounded by an isolation strip varying in width from 2 to 4 m., depending on the size of the plot. A trench was dug around each isolation strip to a depth of 76 cm. to cut off all of the roots from surrounding trees, herbs, and grasses; and each year this trench was remade. In each plot, as well as in the isolation strips, the seedlings were sprayed with Bordeaux mixture at monthly intervals during the growing season (and less frequently during the dormant season) to prevent infection from the brown-spot leaf blight. The seedlings within the plots were all tagged and measured as to height and diameter at the time of establishment of the plots and again at the end of each growing season. In Table 3 is shown the number of seedlings per plot and the treatment and designation of each plot.

MICRO-ENVIRONMENT

EVAPORATION

Livingston spherical porous clay cup atmometers were arranged in pairs (one black and one white) in each plot. The reservoir bottle of each atmometer unit was placed in the ground to its neck so that the center of the

TABLE 3. DENSITIES IN STANDS AND TREATMENTS OF PLOTS

Plot number[1]	Plot		
	Density per acre	Number of seedlings studied	Area per seedling
	Thousands		*Square feet*
O5M	5	100	8.712
U1M	1	100	43.560
U5M	5	100	8.712
U10M	10	200	4 356
U15M	15	225	2.904
U25M	25	200	1.742
U50M	50	200	0.871
U100M	100	200	0.435
D1M	1	100	43.560
D5M	5	100	8.712
D10M	10	100	4 356
D15M	15	225	2.904
D25M	25	100	1.742
D50M	50	100	0.871
D100M	100	100	0.435

[1]Treatment:
O = Natural condition including oaks, herbs, grasses, and pine seedlings—oak plot.
U = Oaks removed, herbs, grasses, and pine seedlings retained—grass plots.
D = Oaks, herbs, and grasses removed; only pine seedlings retained—denuded plot.

evaporative surface of the cup was about 7.6 cm. above ground, and each unit was equipped with a mercury rain-correcting valve. The atmometers were placed so that they would not be shaded by tall trees or snags, but in the grass area it was not always possible to prevent some local shading.

TEMPERATURE

The maximum temperature at the soil surface (about 5 mm. below the surface) was determined by maximum thermometers, which were read each morning. In addition to the thermometers at the soil surface, maximum and minimum thermometers of the Sixe-incubator type were inserted horizontally so that the bulb was 12.7 cm. below the soil surface and the face of the thermometer was exposed in a wooden box with a lid. When readings were taken the lid of the box was removed, the temperature read, and the indicators moved back with a magnet; in this way the bulb of the thermometer was never disturbed. These thermometers were placed in the plots with the extreme densities and in the one with the intermediate density (plots with 1, 25, and 100 seedlings per milacre). In these plots the maximum and minimum temperatures were also read each morning from thermometers placed at 5 cm. above ground. Thus temperatures were obtained at three levels: at 12.7 cm. below the surface, at the surface, and at 5 cm. above the surface of the ground.

At weekly intervals during the growing season and at monthly intervals during the dormant season composite samples of soil were collected from each plot at three depths: 0-5 cm., 5-15 cm., and 15-30 cm. These samples were tested for pH by means of the quinhydrone electrode method, and the soil moisture was determined on oven-dry basis.

ROOT EXCAVATIONS

In order to determine the relationship between the roots of the pine seedlings and the density of stocking, an area was selected on which the site conditions were uniform and on which all the seedlings were of the same age. On this area two milacre quadrats were laid out. On one quadrat there were 24 longleaf pine seedlings, and on the other there were 185 seedlings of the same age. On both milacres the seedlings were in their thirteenth growing season. The vegetation consisted principally of pine forest grasses (*Andropogon scoparius* and *A. elliottii*) and a few legumes, the dominant among which was *Cracca virginiana*. Ruston fine sandy loam was the soil type on both milacres studied. The degree of the intensity of the brown-spot needle blight infection was similar on both quadrats and the seedlings showed indications of heavy periodic defoliation. The only apparently significant difference between the two milacre quadrats was in the number of pine seedlings.

The milacres were marked off and the vegetation on them was mapped. Along the full length of one side of each quadrat was dug a trench a little

over a meter in depth and a meter wide—large enough to permit the free movement of a person. The roots of the pine seedlings were then carefully excavated with an ice pick, measured, and sketched. After a seedling had been completely excavated, it was removed to the laboratory where it was mounted on a large paper marked off in 2½-cm. squares. The measurements of the roots of the seedling were then checked with those on the sketch made in the field, and the seedling was then photographed in the mounted position.

ANALYSIS OF DATA

TEMPERATURE

The average daily temperatures for the growing seasons of 1932, 1933, and 1934 combined are summarized in Table 4. The average maximum temperature at the soil surface was consistently higher in the denuded plots than in the grass plots, but the differences between the maximum temperature on the different plots with the same ground cover did not seem to be consistent.

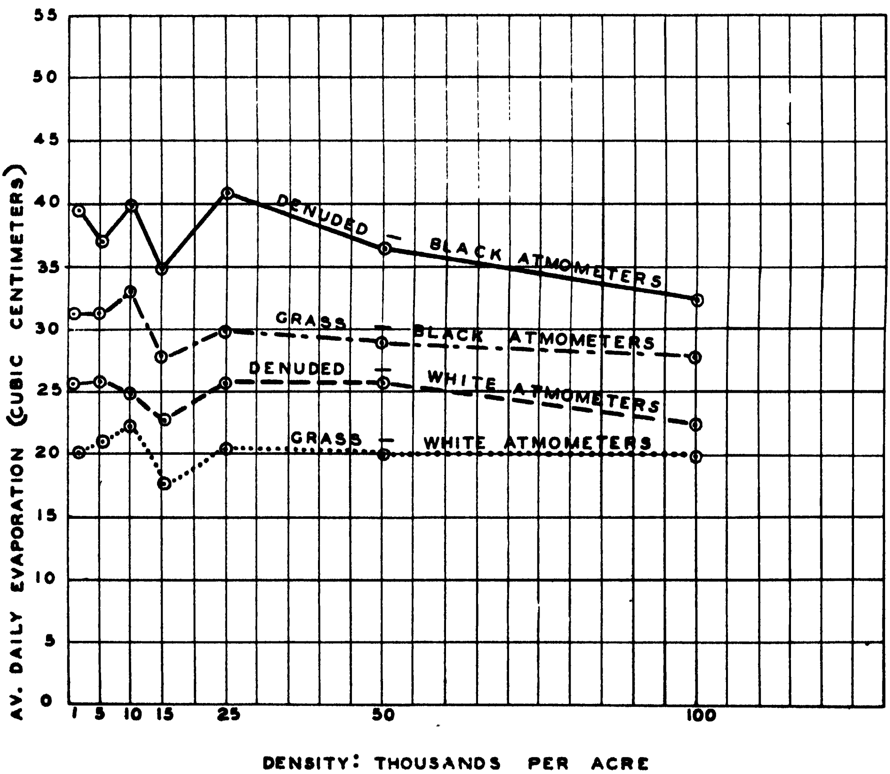

FIG. 3. Average evaporation in cubic centimeters for three growing seasons (1932-1934).

TABLE 4. AVERAGE DAILY MAXIMUM TEMPERATURE, AVERAGE DAILY EVAPORATION, AVERAGE SOIL MOISTURE, AND AVERAGE SOIL ACIDITY FOR THREE GROWING SEASONS (1932, 1933, AND 1934)

Density per acre	Condition of plot	Evaporation				Maximum Temperature						Soil Moisture (percent)						Soil Acidity (pH)					
		Atmometers				Air (°F)		Surface (°F.)		Below surface (°F)		Depth (cm)						Depth (cm)					
		Black (cc)		White (cc)								0-5		5 15		15-30		0-5		5-15		15-30	
		Average	Difference	Average	Difference	Average	Differance	Average	Differance	Average	Difference	Average	Differance	Average	Difference	Average	Differance	Average	Difference	Average	Difference	Average	Difference
1,000	Denuded	39.8	8.4	25 9	5 8	95 5		100 7	8 6	86 1		11 6		12.1		14 1		5 1	0 1	5 1		4 9	
	Grass	31 4		20 1		103 0	7 5	93 1		86 8	0 7	14 2	2 6	14 1	2 0	16 6	2 5	5 0		5 2	0.1	5 0	0 1
5,000	Denuded	37 4	5 9 10 7	26 0	5 0 4 0			103 5	12 4 20.8			11 3		12 2		14 1		5.0	0 1 0 3	4 9	0.3 0 2	4 9	0.2 0 3
	Grass	31 5		21 0				91 1				19 9	8 6 2 3	16 2	4 0 2 6	16 1	2 0 1 8	4 9		4 6		4 7	
	Oaks	26.7		22 0				82 7				17 6		13 6		14 3		4 7		4 7		4.6	
10,000	Denuded	40 1	6 7	25 3	2 7			104 9	15 1			11 2		13 2		14 8		4 8		4 9		4 9	
	Grass	33 4		22 6				89 8				15 9	4 7	13 2		15 2	0 4	5 1	0 3	5 2	0 3	5 0	0.1
15,000	Denuded	34 9	6.7	23 2	5 3			107 2	20 1			12 4		12 0		13 8		4 9		4 9	0 1	5 0	
	Grass	28.2		17 9				87 1				15 8	3 4	13 1	1 1	13 9	0 1	5 1	0 2	4 8		5.2	0 2
25,000	Denuded	41 1	10 8	25 9	5 3	97 4	1 6	100 3	8 3	91 6	6.2	11 2		11 8		13 9		4.8		4 9		4 9	0 2
	Grass	30 3		20.6		95.8		92.0		85 4		16 8	5 6	14 6	2 8	14 9	1.0	4.9	0.1	4 9		4 7	
50,000	Denuded	36.6	7 1	25 8	5 7			100 5	13 9			13 3		13.8		14 6	0.3	5.0		4.8		4 8	
	Grass	29.5		20 1				86 6				16 9	3.6	13 8		14.3		5 0		5 1	0 3	5 0	0 2
100,000	Denuded	32 5	4.2	22.5	2 6	98 4		95 5	5 2	84 1		14 8	0 4	14 2	0 6	15 7	0 6	4 7		4.9		4 8	
	Grass	28 3		19 9		100 2	1 8	90 3		84 1		14 4		13 6		14 9		4 7		5 1	0 2	4 8	

EVAPORATION

The data on the evaporation rate on the different plots are shown in Table 4 and Figure 3. It is at once evident that the average daily evaporation was greater in the denuded than in the grass plots, but there is no definite relationship between the evaporation rate and the density of stocking. Neither in grass plots nor in denuded plots does the evaporation rate vary much with the density. The increased evaporation rate in the denuded plots is probably caused by the higher light intensity and greater air movement than in the grass plots. These factors should also increase the transpiration from the pine seedlings, but apparently such an increase in transpiration did not have a harmful effect on the seedlings, for, as will be shown later, in all cases the seedlings in the denuded plots where the evaporation rate was higher showed a greater increase in growth than did the seedlings in the grass plots. The evaporation data seem particularly significant because they show the influence of ground cover on evaporation in the immediate vicinity of the pine seedlings.

LIGHT

The intensity of the light on the different plots was not measured directly but by using the difference in evaporation between the black and white atmometer cups as an expression of the solar radiation, a figure was obtained which suggests a strong correlation between the light intensity and the density in the stands on the different plots. Assuming that the denuded plot with fewest seedlings had the most favorable light conditions, then the difference between evaporation on the denuded and the grass plots of that density (1 seedling per milacre) probably was due to increased solar radiation on the denuded plot. This difference in evaporation was then taken as 100 percent

TABLE 5. DIFFERENCES IN THE AVERAGE DAILY EVAPORATION BETWEEN THE BLACK AND WHITE ATMOMETERS (SOLAR RADIATION)

Density per acre	Condition of plot	Difference in evaporation between black and white atmometers (cc)	LIGHT INTENSITY (percent)		Oak plot
			Grass plot	Denuded plot	
1,000	Denuded	13.9	. .	100	...
	Grass	11.3	81.3	. .	.
5,000	Denuded	11.4	...	82	...
	Grass	10.5	75.5	....	...
	Oak	4.7	....	....	33.8
10,000	Denuded	14.8	.	106.5	....
	Grass	10.8	77.7	....	....
15,000	Denuded	11.7	....	84.2	. .
	Grass	10.3	74.1	....	...
25,000	Denuded	15.2	...	109.3	...
	Grass	9.7	69.8	....	....
50,000	Denuded	10.8	...	77.7	....
	Grass	9.4	67.7	....	....
100,000	Denuded	10.0	....	71.9	....
	Grass	8.4	60.4	....	....

solar radiation. On this basis, the differences in evaporation between the denuded and the grass plots of the different densities were then computed to indicate the solar radiation on each plot. The data in Table 5 show that in the grass plots the light (solar radiation) definitely decreases with the density of the stand. In the denuded plot this is not as marked as in the grass plots.

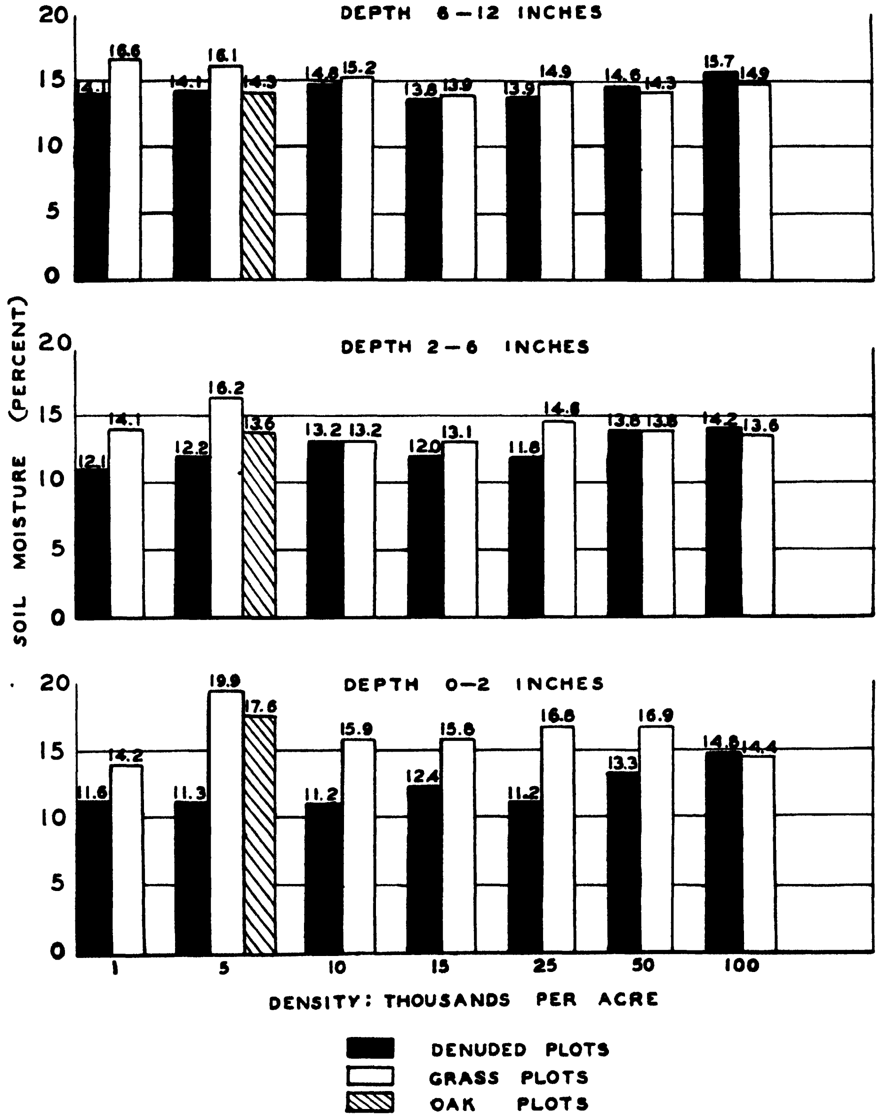

FIG. 4. Average soil moisture on dry weight basis for three growing seasons (1932-1934).

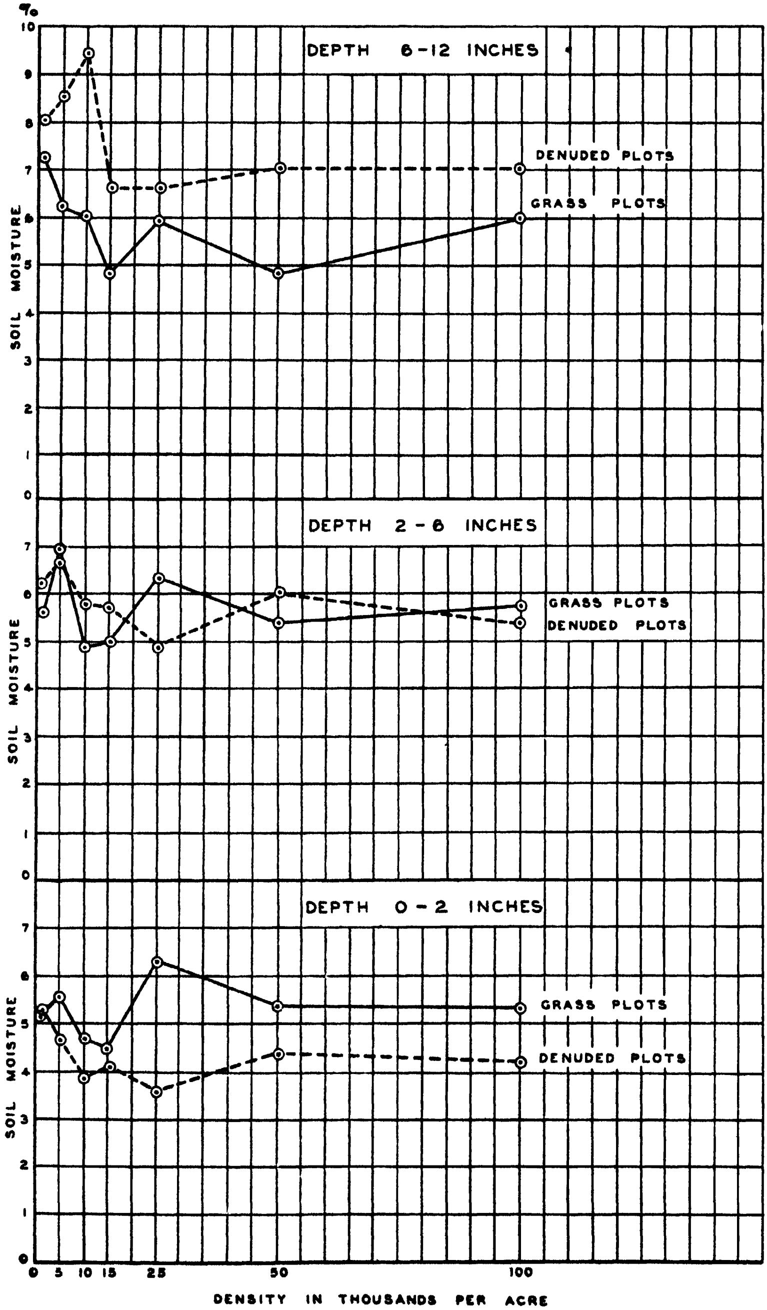

FIG. 5. Average soil moisture in denuded and grass plots during three months' drought—September 4 to December 4, 1933. Total rainfall 2.96 inches.

SOIL MOISTURE

Determinations of soil moisture of composite soil samples taken weekly from each plot during the three growing seasons (Table 4 and Fig. 4) showed that the average soil moisture was less at the surface layer (0-5 cm.) in all denuded plots than in the grass plots, except in the one with 100 seedlings per milacre, where the difference is very small. In the next depth (5-15 cm.), the results were not very consistent, although in general there appeared to be more moisture in the grass plots of the lesser densities than in the denuded plots of the same densities. The same can be said for the soil moisture at the lowest depth (15-30 cm.), although the differences tend to disappear with increasing densities. The differences at this depth between the denuded and the grass plots were very small.

Of particular interest are the data on soil moisture obtained during the period of low rainfall (September 4 to December 4, 1933) when the total rainfall for the 3 months amounted to only 2.96 inches. During this period (Table 6 and Fig. 5) all the grass plots except the one with the least density showed a higher moisture content near the surface than did the denuded plots, but at the lower depths this condition becomes reversed.

In general, the data seem to indicate that under normal conditions soil moisture is adequate for plant growth; the differences between soil moisture of the grass plots and that of the denuded plots are insignificant. A somewhat different condition prevails during a period of low rainfall when the water supply in the soil is low. Then the denuded plots show a slightly lower moisture content in the upper 5 cm. of soil than do the undenuded

TABLE 6. SOIL MOISTURE ON THE PLOTS DURING A PERIOD OF LOW RAINFALL (SEPTEMBER 4-DECEMBER 4, 1933)[1]

Density per acre	Condition of plot	Soil Moisture At Depths					
		0-5 cm	Difference	5-15 cm	Difference	15-30 cm	Difference
				Percent			
1,000	Denuded	5.29	0.10	6.23	0.60	8.13	0.92
	Grass	5.19		5.63		7.21	
5,000	Denuded	4.69		6.75		8.49	{2.25 / 2.92}
	Grass	5.63	{0.94 / 0.04}	6.92	{0.17 / 2.16}	6.24	
	Oak	5.59		4.76		5.57	. .
10,000 . .	Denuded	3.94		5.66	0.73	9.40	3.40
	Grass	4.76	0.82	4.93		6.00	
15,000	Denuded	4.14		5.72	0.76	6.58	1.77
	Grass	4.54	0.40	4.96		4.81	.
25,000 .	Denuded	3.60		4.91		6.61	0.71
	Grass	6.31	2.71	6.26	1.35	5.90	
50,000	Denuded	4.38		5.98	0.69	6.96	2.12
	Grass	5.45	1.07	5.29		4.84	
100,000	Denuded	4.25		5.44		7.07	1.07
	Grass	5.28	1.03	5.77	0.33	6.00	. .

[1]The rainfall during these 3 months amounted to 2.96 inches

plots, but the high moisture content of the soil in the denuded plots at a depth of 15-30 cm. is very marked. At 5-15 cm. the soil moisture curves are intermediate and rather irregular. At the surface, due to high evaporation, the soil moisture content is lower in the denuded plots than in the grass plots, while at 15-30 cm. the roots of the plants in the grass plots draw moisture from the lower depths; when water is plentiful they obtain enough water from the 5-15 cm. level. In the denuded plots, however, both evaporation and the loss of moisture through the seedlings account for the low water content above 15 cm., but the drain on the moisture below 15 cm. is not as heavy as in the grass plots. These data seem to indicate that the competition between grasses and pine seedlings for water is greater when moisture in the soil is low than when the soil contains a sufficient amount of moisture. Scrub oaks, however, seem to exert keen competition for moisture, as is shown by the low moisture content in the lower depths of soil both under normal weather conditions and during droughts.

RESPONSE OF PINES TO DENUDATION AND THINNING

The effect of denudation on the rate of growth of longleaf pine seedlings, which for 12 years had been growing very slowly, was very rapid. Even after one growing season the response was very obvious. The seedlings in the denuded plot with the lowest density (1 per milacre) showed an increase in height in one growing season of over 456 percent. The other denuded plots likewise showed marked increases (Table 7).

After three growing seasons this response was particularly noticeable. There obviously exists a definite correlation between density of the stand and rate of growth of the seedlings. This is especially evident in the denuded plots where the ground cover has been removed in all cases and where the density alone varied. There we find for all height classes the increase in growth is progressively smaller as the densities become greater (Table 8 and Fig. 6).

TABLE 7. PERCENTAGE OF INCREASE IN HEIGHT GROWTH OF LONGLEAF PINE SEEDLINGS IN ONE GROWING SEASON AFTER ESTABLISHMENT OF PLOTS

Density per acre	Condition of plot	Percent increase in height growth
1,000	Denuded	456
	Grass	64
5,000	Denuded	115
	Grass	46
	Oak	0
10,000	Denuded	79
	Grass	33
15,000	Denuded	56
	Grass	31
25,000	Denuded	57
	Grass	23
50,000	Denuded	15
	Grass	27
100,000	Denuded	25
	Grass	18

TABLE 8. SUMMARY OF HEIGHT GROWTH OF TREES ON ALL PLOTS

Density per acre	Condition of plot	ORIGINAL HEIGHT CLASS (in feet): 0.10 (3 cm.)				0.20 (6 cm.)				0 30 (9 cm)				0 40 (12 cm)				0 60 (18 cm)				All classes				Areas per plot (mil-acres)
		Number of trees	Average height 1932	Average height 1935	Percent increase	Number of trees	Average height 1932	Average height 1935	Percent increase	Number of trees	Average height 1932	Average height 1935	Percent increase	Number of trees	Average height 1932	Average height 1935	Percent increase	Number of trees	Average height 1932	Average height 1935	Percent increase	Number of trees	Average height 1932	Average height 1935	Percent increase	
1,000	Denuded	56	12	3 27	2,625	38	17	4.65	2,579	4	.30	6 37	1,990					2	.6	10 10	1,583	98	[1].15	3 16	2,007	100
	Grass	90	.10	.70	600	9	.17	1 67	882													99	.11	80	627	100
5,000	Denuded	82	.13	2.22	1,608	18	18	2 78	1,444													100	.13	2.32	1,685	20
	Grass	83	12	55	358	15	17	.83	388													98	.12	58	383	20
	Oak	66	.11	.22	100	33	.20	.37	85	1	28	70	150									100	15	27	80	20
10,000	Denuded	60	.12	98	718	37	17	1 07	529	1	27	80	196									98	14	1 01	621	10
	Grass	180	11	40	263	16	.18	86	377	2	30	1 55	417									198	.12	45	275	20
15,000	Denuded	106	.10	.81	710	109	18	1 09	506	8	28	1.52	443	1	36	3 10	761					223	[2] 16	.97	506	15
	Grass	191	.12	.37	208	30	18	.58	222	3	.29	77	166									224	.13	.40	208	15
25,000	Denuded	59	12	.73	425	39	.18	80	344	1	.26	3 40	1,208									99	14	.78	457	4
	Grass	174	12	27	125	30	19	39	105													204	13	.29	123	8
50,000	Denuded	80	12	.38	217	20	17	56	229													100	.13	.42	223	2
	Grass.	180	.11	.20	91	17	.18	33	94													196	11	.21	91	4
100,000	Denuded	94	12	.29	141	8	.18	.54	200													102	.12	31	158	1
	Grass	194	.10	.20	100	7	.18	.36	100													203	.11	.20	82	2

[1]The 18-cm. class excluded from computations

[2]The 12-cm. class excluded from computations.

There also appears to be a definite relationship between original height of the seedling and increase in growth. The percentage of increase in growth in the denuded plots was generally greater for seedlings whose original height class was 3 cm. than for those whose original height class was 6 cm., while in the grass plots the reverse seems to be true; the smaller seedlings generally made less growth than the taller seedlings.

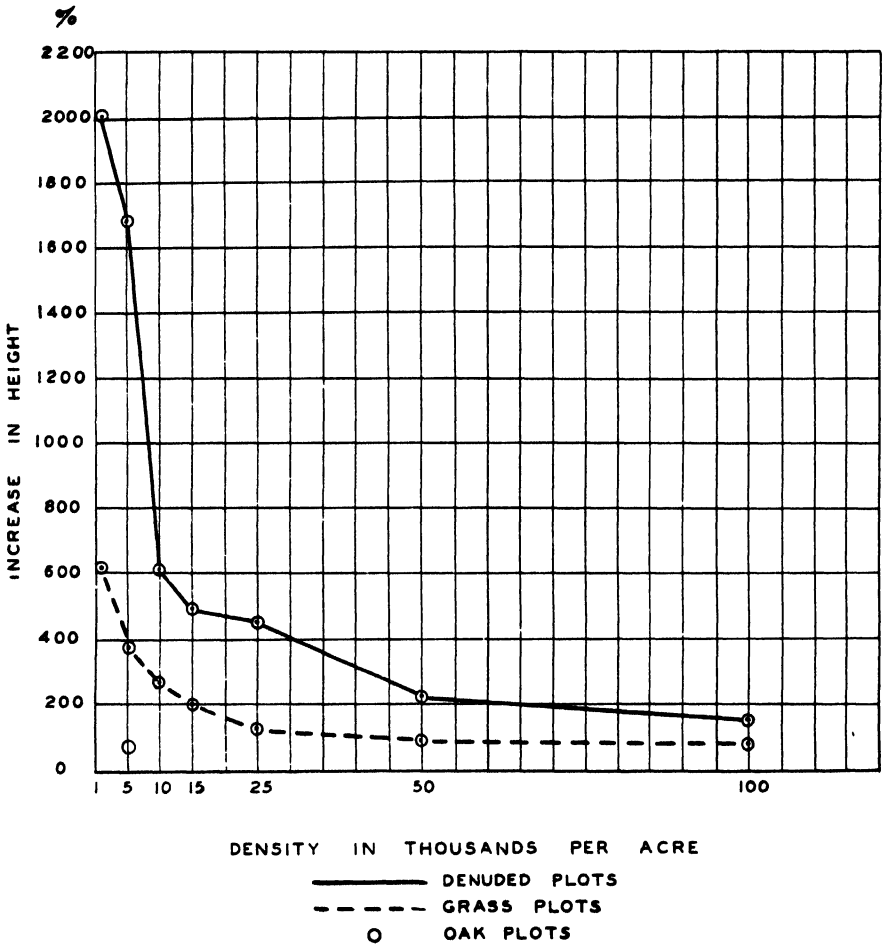

Fig. 6. Increase in height during growing seasons of 1933-1935. Combined 0.10, 0.20, and 0.30 ft. classes.

The combined effect of density and ground cover on the growth of longleaf pine seedlings is just as pronounced. A study of Figure 6 and Table 8 shows that the average increase in growth in the grass plots was much smaller than in the denuded plots, indicating that the ground cover in the grass plots caused retardation of the growth of the seedlings. The most

spectacular increase in growth took place in the denuded plot with the density of one seedling per milacre, where the growth showed an increase of 2,007 percent as against 627 percent in the grass plot. In other words, the difference in the increase in growth between the seedlings in the denuded and those in the grass plots apparently was related to the removal of the ground

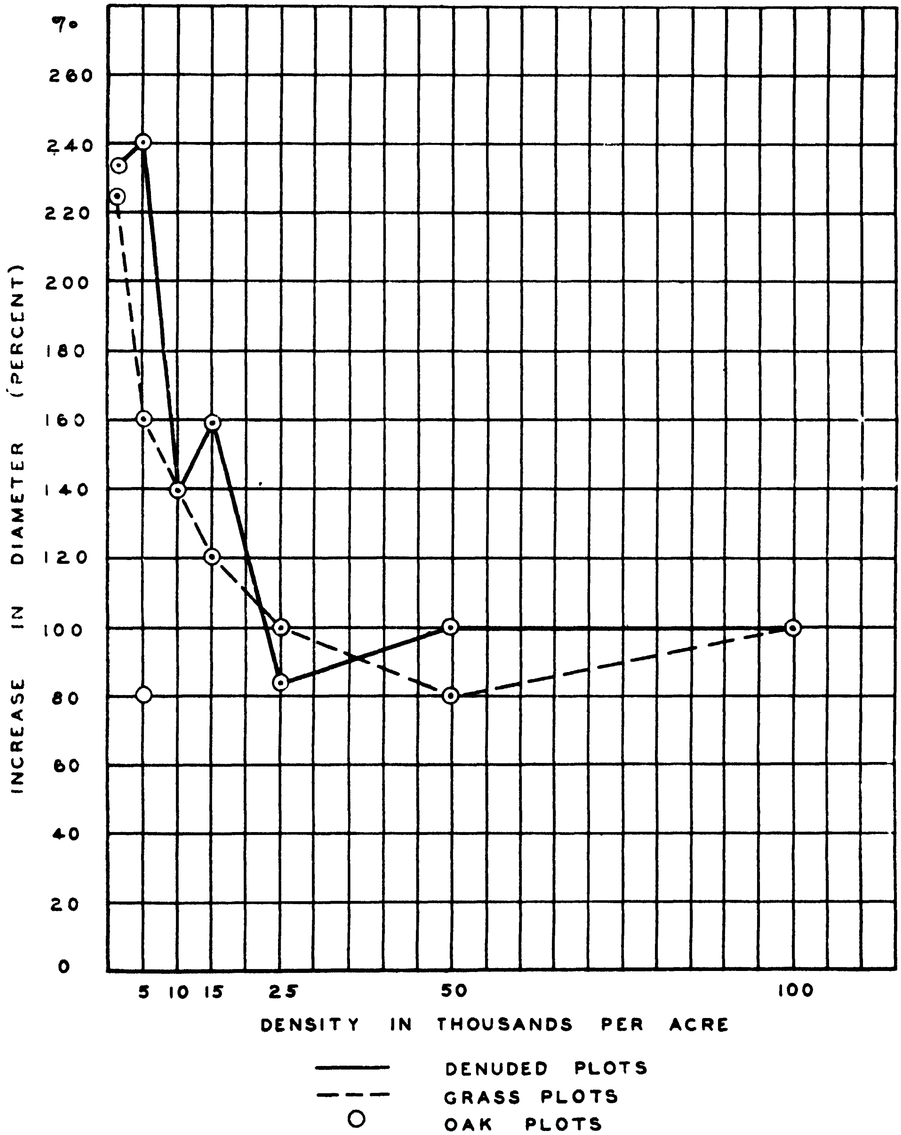

FIG. 7. Increase in diameter of seedlings during growing seasons 1933-1935. Original diameter class 0.3 to 0.9 inch.

cover. The ratios of the increase in growth for the three growing seasons in the denuded plots to that in the grass plots run as follows.

	Thousand Seedlings Per Acre						
Density	1,000	5,000	10,000	15,000	25,000	50,000	100,000
Ratios	4.4:1	4.8:1	2.6:1	3.0:1	4.0:1	2.9:1	2.1:1

The effect of density on stem diameter at the ground level can be seen in Table 9 and Figure 7. In general, the seedlings in the denuded plots made greater growth in diameter than those in the grass plots, but the differences are in some cases too small to justify definite conclusions.

The ratios of the increase in diameter growth of the seedlings in the denuded plots to that in the grass plots are as follows:

	Thousand Seedlings Per Acre						
Density	1,000	5,000	10,000	15,000	25,000	50,000	100,000
Ratios	1.6:1	1.5:1	1:1	1.3:1	1:1	1.2:1	1.2:1

From these ratios it is seen that the effect of density and ground cover on the growth in diameter at the root collar of the pine seedlings is not very evident during the three growing seasons following the treatments.

Of particular interest is the fact that in the plot where the scrub oaks were left undisturbed, the seedlings showed the least growth in height, amounting to only 80 percent in two growing seasons.

DISCUSSION

To summarize, it may be stated that the measurements of the seedlings for three growing seasons following the establishment of the experiment show markedly the effects of both density of stocking and the ground cover on the height-growth of the seedlings. The data seem to indicate that the height-growth of the seedlings in the denuded plots, where the seedlings compete among themselves and where the competition varies in degree with the number of seedlings per acre, is markedly influenced by this competition. The plots with the larger number of seedlings showed a smaller increase in growth than those with smaller numbers of seedlings. The vegetation on the ground apparently acts as a keen competitor, for in the grass plots the growth in height is much less than in the denuded plots, where the ground cover has been removed. Marked evidence of the competition produced by the ground cover is seen in the scrub-oak plot where very little growth has been made during the two growing seasons following the establishment of the plot. One striking fact should be noted here: Many of the trees in the denuded plots in the densities of 1, 5, and 15 thousand per acre possessed fascicles with four and five leaves in each cluster. That is particularly significant, for generally seedlings possess fascicles of two leaves each, and only the more vigorous seedlings possess fascicles with three leaves each. Apparently, denudation has increased not only the height growth but also the

TABLE 9. SUMMARY OF DIAMETER GROWTH OF TREES ON ALL PLOTS

Density per acre	Condition of plot	ORIGINAL DIAMETER CLASS (in inches) 0.3 Number of trees	0.3 Average diameter 1932	0.3 Average diameter 1935	0.3 Per-cent in-crease	0 6 Number of trees	0 6 Average diameter 1932	0 6 Average diameter 1935	0 6 Per cent in-crease	0.9 Number of trees	0.9 Average diameter 1932	0.9 Average diameter 1935	0.9 Per cent in-crease	1.2 and above Number of trees	1.2 and above Average diameter 1932	1.2 and above Average diameter 1935	1.2 and above Per-cent in-crease	All classes Number of trees	All classes Average diameter 1932	All classes Average diameter 1935	All classes Per-cent in-crease	Area per plot (mil-acres)
1,000	Denuded	4	0 3	2.0	567	78	0.6	2.0	233	15	0.7	2.2	214	3	1 0	2.6	160	100	0 6	2.0	233	100
	Grass	12	0.2	1.2	500	87	0.5	1.3	160									99	0 4	1 3	222	100
5,000	Denuded	4	0.3	1.6	433	93	0 5	1 7	240	3	0 7	2 0	186					100	0.5	1 7	240	20
	Grass	0				91	0 5	1 3	160	7	0.7	1.5	114					98	0.5	1 3	160	20
	Oak.	8	0 3	0.7	133	76	0 5	0.9	80	16	0 7	1 1	57					100	0 5	0 9	80	20
10,000	Denuded	6	0.3	0.9	200	86	0 5	1 1	120	6	0 7	1.4	100					98	0 5	1 2	140	10
	Grass	3	0.3	0 8	166	182	0 5	1 2	140	13	0 7	1 4	100					198	0 5	1.2	140	20
15,000	Denuded	4	0 3	1 1	266	204	0 5	1 3	160	17	0 7	1 4	100					225	0 5	1 3	160	15
	Grass	2	0 3	0 8	166	216	0 5	1 1	120	8	0 7	1 2	71					226	0 5	1 1	120	15
25,000	Denuded	3	0 3	1.0	233	78	0.5	1 1	120	17	0 8	1 4	75					98	0 6	1 1	83	4
	Grass	0				186	0 6	1 0	67	14	0 7	1 2	71					200	0.5	1 0	100	8
50,000	Denuded	2	0 2	1.0	400	96	0.5	1 0	100	2	0.7	1 2	71					100	0 5	1 0	100	2
	Grass	6	0 3	0.8	166	186	0 5	0 9	80	5	0 7	1 1	57					197	0 5	0.9	80	4
100,000	Denuded	1	0.3	0.5	67	96	0 5	1.0	100	5	0 7	1 2	71					102	0 5	1.0	100	1
	Grass	5	0 3	0.7	133	198	0 4	0 8	100									203	0 4	0 8	100	2

vigor of the plants. The effect of density and ground cover on the growth in diameter at the root collar is as yet not marked, and the differences in growth in diameter between the seedlings in the denuded plots and those in the grass plots are too small for any conclusions. Another interesting fact is that in the denuded plots with densities of 1, 5, and 10 seedlings per milacre, six seedlings were found bearing pistillate cones on the uppermost branches (Pessin 1936). Four of these were only 1 foot in height and were already bearing pistillate cones, while one was 4 feet high and another 6 feet high.

The stand of pine seedlings on the area selected for the experiment was very heavy, in places as much as 435 to the milacre. Up to the time of the initiation of this study most of the seedlings which were 12 years old were badly infected with the brown-spot leaf blight and all were stunted, so that very few were over 5 cm. in height. The terminal buds were poorly developed on all of them and there were no indications of approaching height growth such as is known in longleaf pine seedlings when the terminal buds assume the characteristic candle-like appearance. To eliminate the factor of disease, all the seedlings were sprayed with Bordeaux mixture and nearly all the leaf blight disappeared by the end of the first growing season after establishment of the plots. The denudation was accomplished initially by hoeing, which during the first season had to be done several times to eliminate the sprouts of the perennials, but in the subsequent growing seasons light hoeing once or twice in the spring of the year usually removed any annuals that had started. Contrary to current belief, longleaf pine seedlings when cut at the surface of the ground sprout out again; it was, therefore, necessary to go over the plots three times during the first season and twice during the second season to eliminate the sprouts from the longleaf pine seedlings which were cut out during the establishment of the experiment. The removal of the oak sprouts did not offer a problem. It was found that when the scrub oaks were cut down in the spring after they were all in full leaf, they usually did not sprout profusely. Although an occasional oak stump would sprout, such juvenile twigs were easily removed, but those oaks which were cut down late in autumn or in winter required periodic removal of the sprouts.

A review of the data reveals that the average evaporation rate was consistently higher in the denuded plots than in the grass plots, but the differences under the same condition of ground cover did not vary significantly from plot to plot (density to density). The solar radiation (measured by the difference in evaporation between the black and white atmometers) was of course higher in the denuded than in the grass plots. The factors which influenced evaporation in the plots also influenced transpiration of the pine seedlings, but no evidence was anywhere present that such increased transpiration had a harmful effect on the pine seedlings. On the contrary, the seedlings in the denuded area showed greater vigor and growth than did those in the grass plots, where conditions for transpiration were less favorable.

Of particular interest is the temperature at the soil surface. In all the plots the average maximum temperature at the surface was considerably higher in the denuded plots than in the grass plots. Although the difference in the average maximum soil-surface temperature sometimes reached as much as 20°, no seedling was found in the denuded or the grass plots where the root collar showed any indication of injury.

The moisture content of the soil in the plots with the different densities did not vary markedly. It is true that the average moisture content of the soil during the three growing seasons was consistently higher in the upper 5 cm. of the soil in the grass plots, except in the plot with highest density, but in the lower depths the data were not consistent. At 15-30 cm. the soil moisture was somewhat higher in the grass plots with densities of 1 to 25 seedlings per milacre, while in the plots with densities of 50 and 100 seedlings per milacre the denuded plots showed somewhat higher moisture content than the grass plots. It is doubtful whether under normal conditions, with an average annual rainfall of over 65 inches, the soil moisture even under the most severe conditions of competition affects the growth of plants. During periods of low rainfall, however, such as existed from September 4 to December 4, 1933, the moisture content of the soil must influence the rate of competition for moisture among plants. The data at hand seem to bear this out. During these 3 dry months, the average soil moisture was lower in the surface layer of the denuded plots than in the grass plots, but the moisture was higher at the lower depth in the denuded plots than in the grass plots, indicating that the roots of the grasses were drawing upon the supply of moisture which would normally be utilized by the pine seedlings. Inasmuch as the drought occurred late in the growing season, however, it is doubtful whether this reduced supply of moisture in the lower depths seriously affected the growth of the pine seedlings.

Both the density of stocking and the denudation doubtless influenced the rate of growth of the pine seedlings in the different plots. The results are clear-cut and definite. These seedlings which were growing in the plots denuded of all vegetation made a phenomenal increase in growth within the brief period of three growing seasons. Even the seedlings with a density of 100 per milacre showed a considerably higher increase in growth than did those in the grass plot with the same density. The greatest growth occurred in the denuded plots with densities of 1, 5, 10, and 15 seedlings per milacre. That the removal of the grass stimulated the growth of the pine seedlings seems obvious, but no data are as yet available which might explain fully this phenomenal growth in the denuded plots.

The effect of the number of seedlings per milacre on the rate of growth of the pines is also very definite. Those crowded the most (100 per milacre) showed least increase in growth, while those in the plot with the lowest density showed the greatest increase.

It is safe to conclude that the ground cover has definitely been an influence in the retardation of growth of the seedlings, but the explanation for this is not so evident. On the basis of the results, one might be tempted to ascribe the cause to the removal of competition from the grass and herbs. But "competition" is an all-inclusive term and is meaningless unless the different factors operating during competition are definitely known. In this case, competition for moisture can be ruled out as an explanation for the slower growth of the pines in the grass plots, for at no time has the moisture content of the soil been critically low. Of particular interest is the fact that in the denuded plots with densities of 1, 5, 10, and 15 seedlings per milacre many trees have fascicles with four and five leaves each. This is especially true of the current growth (1936). Fascicles with two leaves are extremely rare and fascicles with three and four leaves are quite common; while in the grass plots the fascicles usually bear two and three needles per cluster.

Another point of interest is the apparent effect of denudation on cone production. In the denuded plots seedlings as low as 30 cm. were already bearing ovulate cones, which, however, died about June 5; but the fact that such low longleaf pine trees were already bearing cones, while other trees 20 times as high and of the same age were not bearing, is a question that needs further investigation.

ROOT STUDIES

The relationship between the root systems of the pine seedlings growing under different degrees of density (Pessin 1935) is of interest in connection with this study. The measurements of the excavated pine roots in plots with different densities are shown in Tables 10 and 11 and in Figure 8. The height of the excavated seedlings in the milacre with 185 seedlings varied from 0.6 to 3.1 inches, averaging 1.5 inches, whereas the length of the tap-

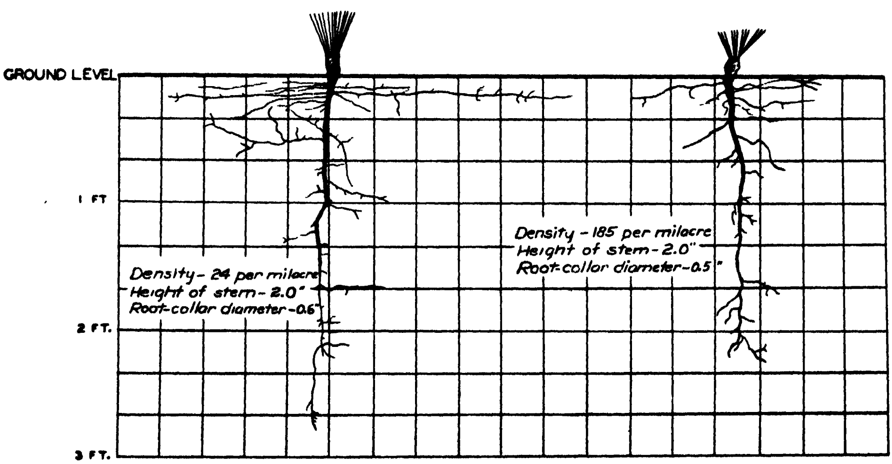

FIG. 8. Roots of longleaf pine seedlings 13 years old grown under same site conditions but in stands of different densities.

roots varied from 15.8 to 4.8 feet, averaging 2.3 feet, or about 18 times greater than the average length of the stem. Seedlings averaging 1.5 inches in height had an average total length of lateral roots of 5.4 feet and an average number of 26 lateral roots.

The height of the pine stems in the quadrat with the 24 seedlings per milacre varied from 0.98 to 4.02 inches, averaging 1.97 inches for the 21 seedlings excavated; whereas the length of the taproot varied from 1.3 to 5.5 feet, averaging 2.8 feet, or about 17 times greater than the average length of the stem. The average seedling, 1.97 inches in height, had an average total length of lateral roots amounting to 7.3 feet, with an average number of 31 lateral roots.

When the 19 seedlings excavated in the milacre with 185 seedlings were arranged by height classes, 10 seedlings fell in the 1.0-inch class, 7 in the 2.0-inch class, and 2 seedlings in the 3-inch class. The average length of the taproot for the first class was 25 times the length of the stem, for the second class 15 times, and for the third class 9 times the length of the stem, indicating that the ratio of the length of taproot to that of the stem decreases as the stem increases in height. The number of the lateral roots became greater

TABLE 10. ROOTS OF LONGLEAF PINE SEEDLINGS
Location: Bogalusa, Louisiana. Density: 185 seedlings per milacre. Age: 13 years.

Height of seedlings	Diameter of seedlings	Length of taproot	Number of lateral roots	Total length of lateral roots	Depth of occurrence of most lateral roots
Inches	*Inches*	*Feet*		*Feet*	*Feet*
0.6	3	1.3	9	8	.7
1.0	5	2.8	16	3.8	7
1.0	5	3.2	22	4.5	3
1.0	6	2.3	41	6.0	5
1.0	4	1.3	15	1.7	.7
1.0	5	3.0	47	11.4	1.0
1.1	4	2.8	22	4.6	7
1.1	.3	0.6	13	3.4	7
1.4	3	1.3	9	6	.7
1.4	5	2.2	23	2.7	.7
1.8	5	1.3	11	6	.7
1.8	6	3.3	18	3.0	.7
2.0	.4	4.8	29	7.0	.7
2.0	4	1.8	21	5.3	.8
2.0	5	2.2	31	5.3	.5
2.1	4	1.9	44	5.1	1.0
2.2	7	2.5	41	10.5	.3
2.7	.6	1.7	31	9.2	1.7
3.1	8	2.9	44	17.8	1.0
Average 1.5	.5	2.3	26	5.4	7
Height class	**Number of trees**	**Average**			
Inches		*Feet*		*Feet*	*Feet*
1.0	10	2.1	22	3.9	.6
2.0	7	2.5	28	5.2	7
3.0	2	2.3	37	13.5	1.3

as the height of the stem increased. The average number of lateral roots for the 1-inch class was 22; for the 2-inch class, 28; and for the 3-inch class, 37. The total length of the lateral roots also showed a definite relationship to size of stem. The lateral roots of the pine seedlings in the first class showed an average total length of 3.9 feet, those of the second class 5.2 feet, and those of the third class 13.5 feet.

TABLE 11. ROOTS OF LONGLEAF PINE SEEDLINGS
Location: Bogalusa, Louisiana. Density: 24 seedlings per milacre. Age: 13 years.

Height of seedlings	Diameter of seedlings	Length of taproot	Number of lateral roots	Total length of lateral roots	Depth of occurrence of most lateral roots
Inches	*Inches*	*Feet*		*Feet*	*Feet*
3.0	.8	2 2	59	11.2	3
1.5	4	2 2	33	3.8	1.3
1.5	5	1.5	27	3 8	.8
2 0	6	2 0	40	6 3	.8
4.0	.7	4 9	55	9 0	2 0
1.7	.6	2.7	22	9 6	1 0
4.0	.6	5 2	36	9.5	5
1 7	.6	2 1	22	8.9	1 5
2 0	5	3 7	19	8 8	.3
2.0	6	2 7	40	9.2	7
2 0	.6	2 5	31	9 7	1 0
1.6	7	2 5	36	7.3	5
2 0	.4	1 9	22	3.8	1.0
1.0	4	2 3	12	0 8	0 3
1 5	.5	3 3	16	6 3	0.3
1.8	.6	2 3	33	10.6	2 0
1.8	6	5 5	41	11.2	0 6
2 0	5	3 5	25	5 6	2 0
1.9	.6	1 3	28	5 0	0 7
1.2	5	2 8	22	4 5	1 0
1.7	6	2.3	34	8 3	1 6
Average. 2.0	.6	2 8	31	7 3	1.0
Height class	**Number of trees**	**Average**			
Inches		*Feet*		*Feet*	*Feet*
1 0	5	2 4	22	3 8	7
2.0	13	2.7	30	8.0	1 5
3.0	1	2.2	59	11 2	3
4 0	2	5.0	45	9.3	1 3

When the 21 seedlings from the low-density quadrat were arranged in height classes (Table 11), here, also, the number of lateral roots was proportional to size of seedlings, but whereas in the dense quadrat most of the seedlings fell in the 1-inch class, here most of the seedlings fell in the 2-inch class. This indicates that the density of the stocking had a retarding effect not only on the growth of the stems but also on the development of the root system, which in both the pine seedlings and the grasses is limited mainly to the top 30 cm. of soil.

SUMMARY

1. Experimental plots were established in 1932 in southeastern Louisiana in an area occupied by 12-year-old longleaf pine seedlings which were still in the grass and showed no evidence of height-growth.

2. The objects of the experiment were to determine the effect of the density of stand and the effect of ground cover on the rate of growth of the pine seedlings.

3. Altogether 15 plots were established. Seven plots with densities of 1, 5, 10, 15, 25, 50, and 100 seedlings per milacre were denuded of all herbaceous cover, shrubs, and other trees. Seven plots were thinned to the same densities and the herbaceous cover was left undisturbed, but the scrub oaks were removed. In the last plot all the herbaceous cover and the scrub oaks were left undisturbed and the seedling stand thinned to five pines per milacre. Each of these plots was surrounded by isolation strips, and a trench to eliminate roots from outside the plot was dug around each isolation strip. The seedlings in each plot were measured at the time of the establishment of the experiment and again at the end of each growing season.

4. Weekly records were taken of evaporation on each plot at 7.6 cm. above the surface of the ground. Samples for soil-moisture determination were also taken weekly at depths of 0-5 cm., 5-15 cm., and 15-30 cm.

5. Temperatures were recorded for the whole area by a Friez hygrothermograph placed 60 cm. above the ground. Maximum temperatures were also recorded daily during the growing season at 5 cm. above the ground, at the soil surface, and at 12.7 cm. below the surface of the soil.

6. The average soil moisture during the three growing seasons seemed consistently higher at the surface in the grass plots than in the denuded plots, except in the plots of greatest density, where the grass plot showed a soil-moisture content slightly less than the denuded plot. At 5-15 cm. the differences in soil moisture between the denuded and the grass plots were not consistent. At 15-30 cm. the soil moisture was somewhat higher in the undenuded plots that were least dense, whereas in the plots with the high densities (50 and 100 per milacre) the denuded plots showed a somewhat higher moisture content than the undenuded plots.

During a drought the average moisture content of the soil at 0-5 cm. below the surface was higher in the grass plots than in the denuded ones, but at 15-30 cm. the denuded plots showed a consistently higher moisture content than the grass plots.

7. The results indicate that as the density increased the growth in height of the seedlings during three growing seasons definitely decreased both in the denuded and in the grass plots.

8. The average increase in height growth of the longleaf pine seedlings in the denuded plots was greater under all densities than in the grass plots. The average increase in height in plots with 1 and 5 per milacre was nearly

five times that in the grass plots of the same density. Even in plots with the highest density (100 per milacre), the increase in growth was twice as much on the denuded plots as on the grass plots.

9. Roots of seedlings of longleaf pine in their thirteenth growing season were excavated in two milacres, in which the densities were 185 and 24 seedlings per milacre. Measurements of the roots indicate that the density of stocking not only influences the growth-rate of the stem, but also the growth-rate of the root system. It is also evident that during the few years following germination, the growth of the taproot is much more rapid than that of the stem. After height growth commences, the growth of the taproot slows down, possibly due to the fact that the roots reach unfavorable soil conditions.

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ECOLOGICAL MONOGRAPHS

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THE INTERRELATIONS OF HABITAT, GROWTH RATE, AND ASSOCIATED VEGETATION IN THE ASPEN COMMUNITY OF MINNESOTA AND WISCONSIN[1]

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[1] A thesis submitted in partial fulfillment of the requirements for the degree of Doctor of Philosophy at the University of Minnesota, in June, 1931.

CONTENTS

THE INTERRELATIONS OF HABITAT, GROWTH RATE, AND ASSOCIATED VEGETATION IN THE ASPEN COMMUNITY OF MINNESOTA AND WISCONSIN

INTRODUCTION

Differences in habitat, even within distances of a few feet, in what seems to be a uniform environment, are characteristic of the natural conditions under which plants grow. The significance of such differences in plant occurrence and growth is as yet largely a matter of conjecture. The measurement of the growth of trees and stands and the identification and enumeration of plant indicators and plant communities are relatively simple, and comparatively satisfactory methods of evaluating them have been developed. But trees and plants are influenced in occurrence and growth by all the factors of their immediate environment. Could these be equally well evaluated, they would provide an integrated measure of habitat and a possible means for quantitative comparison. How this may be accomplished for the aspen community is considered here. The problem is to correlate certain measures of growth with the occurrence of plants associated with the aspen, and thereby to achieve a quantitative measure for the evaluation of the differences between given aspen habitats and their relative productivity. Conversely it will be possible to test the usefulness of habitat features as a means of predicting growth rate of aspen.

The complexity of any plant habitat needs no proof. It is only necessary to enumerate some of the multitude of factors involved, such as illumination and radiation, precipitation, atmospheric humidity, evaporation, air and soil temperatures, moisture, soil texture and structure, and chemical and biological complexes. The host of microorganisms in the upper layers of the soil—many of them chemists of high attainments whose activities vary greatly diurnally and seasonally—contribute to make the soil an inextricably complex and ever-changing feature of every plant habitat. At times, and where one of the factors may become critical in the continued existence of the plants, its significance may be interpreted by means of instrumental and laboratory determinations. Much the commoner circumstance, however, and the one which nearly always obtains in the aspen community, is an intermingling of all these factors in which no one is limiting. Here the combination and interpretation in terms of a scale of habitat productivity for the growth of plants must be attempted by some other means.

Such a problem might be attacked from several different angles. Samples of the different aspen habitats could be collected and analyzed to determine the physical, chemical, and biological properties of the soils. The climatic

environment could be measured instrumentally and the growth of aspen phytometers recorded for these same combinations of factors both in the laboratory and in the field. Similar records for artificial habitats in which the factors of the environment would be controlled might be attempted. These methods are, however, time-consuming and there is always a question of how accurately the conclusions can be applied to the numerous natural habitats which have not been sampled and in which the combinations of factors are different and more or less unknown. Sufficient representative permanent quadrats on which records of growth, vegetation, and environmental factors could be made periodically would serve the purpose admirably; but these would be prohibitive in number—no less than in range of distribution and period of record required.

Another method may be called the biometric, in which samples of the different aspen communities and their habitats are taken and described in quantitative and qualitative terms such that the material may be classified in numerical or other categories and conclusions drawn by biometric analysis, due regard being given to the variations exhibited and the consequent degree of reliability that may be assumed for the biometric measures. This method has the advantage that a large number and wide variety of aspen communities may be sampled in a relatively short time and, if the sample areas cover the range of variation adequately, the conclusions, within determined limits of accuracy, may be applied with some confidence to the whole aspen community in the region. This method was adopted in the present study.

Appreciation and grateful acknowledgment are due to William S Cooper whose advice and encouragement have been genuinely helpful, to C. Otto Rosendahl for assistance in the identification of the plants, to the late J. Arthur Harris and to Alan E. Treloar for advice in the use of the biometric methods, and to Raphael Zon and Henry Schmitz for permission to use the field data from a cooperative study of aspen by the Lake States Forest Experiment Station and the Division of Forestry, University of Minnesota.

COLLECTION AND COMPILATION OF DATA

The essential features of the aspen community have been described elsewhere (Kittredge and Gevorkiantz 1929), but may be here briefly summarized. The aspen community is considered to include only stands in which *Populus tremuloides* Michx. predominates. A very large proportion of the aspen stands in Minnesota and Wisconsin have originated as suckers or offshoots from the roots of a previous stand which was destroyed by fire. The new generation starts promptly and densely from the old established root system. The growth is rapid even in the first year and enables the aspen to take and maintain throughout its 40 to 70 years of vigorous development a dominant position with respect to other vegetation. Thus the trees in any given community are almost all within two or three years of the same age and

have only a minor proportion of other tree species in association with them in the dominant canopy.

The aspen community occurs abundantly and under a wide variety of conditions throughout northern Minnesota and Wisconsin. It is, however, rarely found, if at all, on dry sandy outwash formations and the less favorable peat deposits. It commonly occurs on all the other geological formations from sandy moraine to lake-bed clay, and on a large majority of the soil types of the region. This universality of occurrence makes the aspen a most advantageous community to use as a measure of different habitats.

METHODS OF COLLECTION

The field data were collected largely in 1925 and 1926 under a detailed plan designed for a somewhat more comprehensive forestry project. The pertinent portions of the plan are included in the following paragraphs. Two of the objectives of the project were: (1) To determine the possibilities for the conversion of the aspen type to one of more valuable species such as white pine, white spruce, black spruce, Norway pine, or balsam fir; and (2) to prepare tables for the aspen type to give some idea of its growth and yield and to serve as an index of site for the better soils of the region.

Temporary sample plots were selected to represent areas on which conifers had become established or were coming in under stands of aspen, and also well-stocked stands comprising as far as possible the range of site classes for aspen in the region. The plots or sample areas were one or more chains square, most of them being squares of 0.1 acre. The areas were laid out on the ground with a steel tape and compass, and so located as to represent uniform conditions of vegetation and habitat within the boundaries insofar as that was possible. The selection was limited to areas in which aspen 15 years old or older predominated among the tree species.

Measurements included diameters of all trees more than 0.5 inch d.b.h.[1] and heights of a sufficient number of trees for the construction of a curve of height on diameter for the range of diameters on each plot. Wherever possible, a few heights were also measured in stands of different densities at the same age and on the same site, to determine the effect of density on the site index. Diameters were measured with a diameter tape and heights with a Forest Service or Klaussner hypsometer. Ages were determined with an increment borer from not less than three borings in trees of approximately average diameter at heights of 1 foot above the ground or at 4.5 feet where butt rot occurred.

Where conifers less than 0.5 inches in diameter were present they were recorded by numbers of each species on a quarter-chain strip (16.5 feet wide) through the center of the plot. The ages of conifers of different sizes and species were determined by cutting or boring.

[1] D.b.h. = diameter at breast height, or at 4.5 feet from the ground.

Crown density of the overstory was estimated in tenths of total area. Shrubby and herbaceous vegetation was estimated on a similar scale based on area covered by all species combined and by the important individual species. Other species which constituted an unimportant part of the total were noted.

Soil notes included thickness of litter and humus, and texture, color, and thickness of each distinct horizon of mineral soil to a depth of 3 feet. Soil texture was determined by the appearance and feel of a sample. Topography, slope and aspect, and surface geological formation were also noted; in Minnesota the geological notes were checked by Leverett and Sardeson's maps (1915, 1917). Finally, notes were made as to the probable origin and history of each sample area, and as to any evidence of the subsequent occurrence of fire or other disturbing agencies.

If the data had been collected specifically for the kind of analysis attempted in the following pages, the methods would have been amplified or intensified in several respects. For example, the vegetation might have been evaluated more exactly by quadrat enumeration and more completely to include infrequent or inconspicuous species; soil notes might have included structural features of the different horizons and field determinations of acidity and lime, making possible in some instances more exact assignment of soils to the right soil types; and field work might have been made more uniform by the use of a single crew. However, it has appeared as the analysis has proceeded that the field data, with the exception of that from occasional plots which were obviously incomplete in some respect, are surprisingly satisfactory considering the manner and purpose of their collection.

An unforeseen difficulty, which is inherent in the natural distribution of the aspen community, is the fact that desirable sample areas from the point of view of the vegetation are disproportionately likely to be found on the narrow transitional strip between upland and swamp. This strip, being also transitional between two soil groups or types, is therefore difficult to assign to either one of them with confidence. Plants from both the adjacent habitats tend to intermingle in such situations with resulting confusion of indicator significance. In the early part of the work no attempt was made to avoid these areas.

As the field work progressed, a cumulative record was made of the number of plots obtained in different age and site-index classes. Toward the end special effort was devoted to finding and sampling communities belonging to the classes least well or not at all represented up to that time. This provided at least a moderate number of sample areas in each of the classification categories used, although it probably destroyed the value of the data as representative of any actual proportional distribution of the aspen community among the different habitats in the region.

QUANTITY AND DISTRIBUTION OF DATA

A total of 277 sample plots were available for analysis, of which for most of the particular phases of the analysis only a few were unusable because of gaps in the data recorded. They represent a range of density in aspen stands from heavily overstocked to decidedly understocked. Ages from 16 to 75 years are well represented, and there is one sample each of ages 85 and 95. Site-index values are well distributed from 41 to 82. The nine principal geological surface formations are all represented and each of them may be subdivided, with the exception of the peat, into the red or Early Wisconsin and the gray or Late Wisconsin epochs. Eight soil-texture classes had a sufficient number of samples to permit the distinction of red and gray drift areas in each of them. Fifty-four soil types are represented, although several of them by only one or two plots. The material is not sufficient for an analysis of all the individual soil types, but when the soils are condensed into 22 profile groups a reasonable number of plots are available for most of the groups, and when these plots are assigned to the 16 plant-indicator groups a sufficient number fall into each for moderately satisfactory treatment.

The fact that the material can be classified satisfactorily in these several independent ways, seems to indicate that most of the major variations of the aspen community and of its environment in the region are represented by at least a few sample plots. The actual number of plots which fall in each of the categories of these various classifications will appear in the graphs and tables in which the interrelationhips are analyzed.

In addition to the categories already mentioned, geographic distribution has some significance. The map, figure 1, shows the approximate location of the plots. Although by no means uniformly spaced, their distribution suggests that the chief variations due to geographic location within the territory under consideration have been sampled.

RELIABILITY OF DATA

That the data are probably not numerically representative of the relative occurrence of the aspen community in the different age and site-index classes in the region, has been explained as due to the special effort to find samples of the less frequent classes. It would certainly be unsafe to conclude that, because 20 percent of the plots have site indices lower than 55, the same proportion of the aspen community in the region is on correspondingly poor sites. Similarly, a statement that 20 percent of the aspen in the region is over 57 years old, as it is in the plots, would certainly be a gross exaggeration.

The relation between age and habitat distributions is probably somewhat biased also for a biological reason. No samples could be found of the older age classes on the less favorable habitats—those of site index lower than 55. This coincides with the observation that aspen dies on the poorer sites before

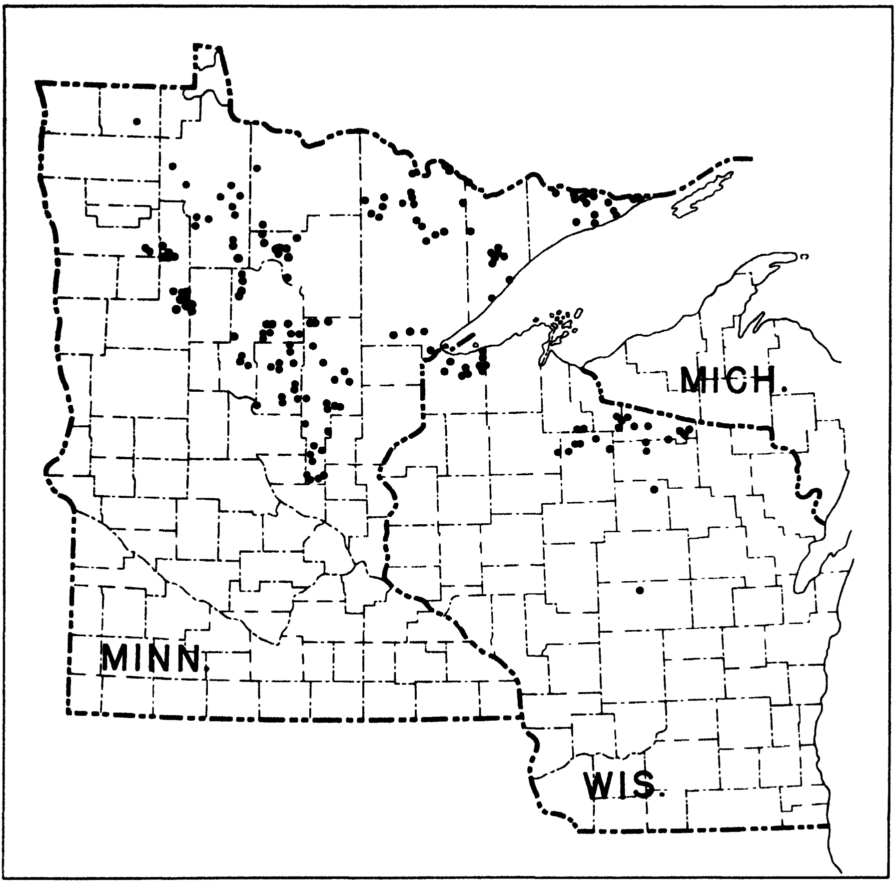

FIG. 1. Location of aspen plots in Minnesota and Wisconsin.

it reaches ages of 50 or 60 years, whereas it commonly attains ages of 75 years or more on the better sites. Whether this is due to lowered resistance to the prevalent fungus disease caused by *Fomes igniarius* (L.) Gillett, or to reduced vigor and inability to function physiologically under adverse habitat conditions, has not been determined (Schmitz and Jackson 1927). Fortunately, this bias has little significance in a study where age is not one of the variables used. It probably does affect to a slight degree the trends of the upper portions of the curves of dominant height over age and volume over age, from which the site-index and volume-index classifications were derived. Even so, the resultant earlier flattening of these curves would not affect appreciably the assignment of plots to site-index or volume-index classes. It would only tend to reduce slightly the range of these two variables at the upper ends of their distribution.

The present material, from whatever angle analyzed, shows that variations between individual measurements or plots are inherent in this as in all biological populations, no matter how homogeneous they may be. This is true of the heights of the dominant trees measured and averaged to obtain the site-index figure for a plot. It is true of the site indices of different plots in what is supposedly a uniform soil type or soil or vegetation group, and it is true of the frequency of occurrence of plant species in what appears to be a uniform habitat group. Biometric analysis enables the evaluation of the significance of means or other measures which may be derived from this variable material and used as the basis for conclusions. Two examples will make this clearer.

Soil profile groups 14 and 19 (to be shown later in figure 15) each contain five plots, the former with site indices from 59 to 66, and the latter from 65 to 78. Comparisons of the means and standard errors are given in table 1.

TABLE 1. MEANS AND STANDARD ERRORS OF SOIL PROFILE GROUPS 14 AND 19.

Item	Group 14	Group 19
Mean site index (M_I)	62.8	71.0
Standard error of mean (σ_{M_I})	± 1.15	± 2.7
Standard error, percent	± 1.8	± 3.8
Twice standard error of mean	± 2.3	± 5.4
Twice standard error, percent	± 3.6	± 7.6

The standard errors were computed by Fisher's (1930) formula,

$$\sigma_{MI} = \frac{\sigma_I}{\sqrt{n-1}}$$

When the probabilities are adjusted by means of "Student's" (1925) tables of the probability integral of his "t" function to allow for the small number of cases, the foregoing figures may be interpreted in several ways. First, with standard errors of 1.15 and 2.7 the chances are 62 in 100 that the true mean of soil-profile group 14 lies between 61.7 and 63.9, and of group 19, between 68.3 and 73.7. The chances are the same that the true mean site index of group 14 is not in error by more than 1.8 percent and of group 19 by more than 3.8 percent. Or, if twice the standard error is used as the criterion, the chances are 88 in 100 that the true mean site index for group 14 lies between 60.5 and 65.1 and of 19, between 65.6 and 76.4, corresponding to a percentage error not exceeding 7.6. This 7.6 may be compared with the 3.6 for group 14, indicating that the latter as an average is decidedly more reliable than the former simply because the variations in the site indices of the individual plots have a narrower range, although their number is the same.

All the means and other biometric measures used in the following pages are subject to varying degrees of reliability in the same way, but these variations are taken into account in the methods themselves, not only for single measures but in comparing the differences between overlapping series of values. Twice the standard error in the normal distribution, corresponding

to a probability of 0.05, is a satisfactory limit used by most workers in deciding whether a computed measure may or may not be due to chance. The use of this criterion will appear frequently in the subsequent analyses of various groupings.

METHODS OF COMPILATION

The average height of the dominant and codominant trees of each plot was computed from the field notes and the corresponding site index obtained. Average ages were derived from the borings of sample trees. Number of trees per acre was used as a measure of density or stocking, and the volumes of the stems of the trees on a per-acre basis were computed by the use of volume tables (Kittredge and Gevorkiantz 1929). The soil categories were checked by the use of geological or soil survey maps insofar as possible. Plant identifications were checked wherever specimens had been collected. These computed values, the soil categories, and the species of vegetation for each plot were then transferred to cards to facilitate sorting into the several categories of which relationships were to be analyzed.

After a sorting of all plots into the groups to be studied, the values of individual plots in each group were plotted on dot diagrams so that the variation within each group and the relations between groups could be roughly evaluated by observation. Plots which had extreme and therefore possibly erroneous values in any group were then rechecked as to these values.

No values were discarded simply as extreme. Differences in numbers of plots basing different analyses are due rather to such omission or inadequacy of certain items of record in the field notes that the plots could not be used satisfactorily in certain specific classifications.

For parts of the plant indicator analysis a separate set of card records was set up, one card for each plant species found in the aspen community. On these cards were entered the data as to the number of occurrences of each species in other communities than aspen and on different soil types. This permitted groupings of species independent of their associations in any particular aspen plot. The records of occurrence of species in communities other than aspen were taken in part from field work by the writer in 1930, in part from published records by Cooper (1913), Gates (1912), Bergman (1923), Stallard (1929), Livingston (1905), Ruthven (1906), and Grant,[2] and in part from vegetation lists from different forest types taken by Gevorkiantz and other members of the Lake States Forest Experiment Station. Although this material was not all homogeneous or entirely satisfactory, it did in the aggregate provide a definite and reasonably reliable means of grouping the species found in the aspen community according to their most common occurrence in some other natural community.

Biometric methods have been used as tools for the testing of hypotheses

[2] Grant, M. L. The burn succession in Itasca County, Minnesota. 63 pp. [Master's thesis, Minn. Univ. Multigraphed.]

or for the determination of degree of relationship, the homogeneity of groupings, or the significance of differences. They do not in any sense replace the logic of biological relationships, nor do they in themselves provide interpretation of results. They facilitate such interpretation by giving a quantitative basis for it. The soils and plant indicators are at present expressible only in categorical terms, and analysis of such data has required the use of methods like those of the correlation ratio and the contingency coefficient. These methods have been fully described and tested in the literature of biometry and statistics. The early stages of the work were discussed in conferences with the late Dr. J. Arthur Harris. Considerable use has been made of the adaptations of method and tables for the application of biometric measures to small numbers of cases by Fisher (1930).

THE REGION

The geographic location and boundaries of the region from which the data came may be seen from the map, figure 1. Roughly, it lies in northern Minnesota and adjacent Wisconsin east and north of Marshall, Wadena, and Benton counties in Minnesota and north of Rusk, Taylor, and Langlade counties in Wisconsin.

CLIMATE

The climate of this section is, in the main, uniform. The mean annual precipitation ranges from 23 inches at the western edge to 40 inches in northwestern Wisconsin. For the most part it is between 30 and 35 inches, of which 20 to 25 inches falls in the growing season between April 1 and September 30. The snowfall is heavier and of longer duration adjacent to and north of Lake Superior, where it may exceed 100 inches, as compared with 45 inches in the western part. The mean annual temperature at International Falls is 35° F. compared with 41° at Milaca, Minn. Maxima of 90 to 100° F. occur in most summers. The growing season or period between first and last killing frosts varies from slightly less than 100 to more than 125 days a year, although frosts may occur occasionally in any of the summer months. The boundary between the Transition and Canadian zones, as defined by Merriam (1894) by a mean daily summer temperature summation of 10,000° F. and a mean for the 6 weeks (June 23 through August 7) of 64.4°, passes across the southern portion of the section. The precipitation-evaporation ratio of Transeau (1905), as computed for individual stations by Livingston and Shreve (1921) at Duluth, is 1.30; and at stations not far outside the region is as follows: Pembina, N. Dak., 0.92; Moorhead, 0.95; St. Paul, 1:02; and Marquette, Mich., 1.33. The range within the region is probably between 1.05 and 1.40. On the whole, the differences between different parts of the region are not of such magnitude as to cause variations in tree growth, vegetation, or soils greater than might be found in closely adjacent habitats of contrasting local environments.

GEOLOGY

Only the essentials of geological history as they influence the local habitats on which sample plots were taken will be outlined. In northeastern Minnesota in a belt south of the Canadian boundary—in places as much as 50 miles wide—the granites, gneisses, and schists of the Huronian and Laurentian periods outcrop freely and are little or not at all covered by glacial deposits. Elsewhere in the region the plot locations were on the unconsolidated Pleistocene deposits, which vary from a few to more than 200 feet in thickness. The earlier Kansan drift is covered by that of more recent age except in unimportant exposures along the larger stream valleys.

The Early Wisconsin glacial invasion came from the area of igneous rocks to the northeast and completely covered the region with a mantle of drift, except as the rock was scoured and left bare in northeastern Minnesota. This deposit is known as the red drift by reason of its color and is characteristically rather stony, low in lime content, and acid in reaction. Two lobes of this advance of the ice occurred in the region, the Patrician in east central Minnesota, and the Chippewa in west central Wisconsin. The more or less intermittent retreat of this ice sheet and the waters from its melting account for the variety of glacial surface formations of the eastern part of the region.

In Western Minnesota, a later invasion of ice, known as the Late Wisconsin or gray drift, advanced from or across the sedimentary formations including limestone to the northwest of Minnesota. This ice partly covered the earlier deposits with a layer of less stony drift having a relatively high lime content and less acid reaction. Postglacial stream cutting, deposition of alluvial material, and accumulation of peat have taken place since the retreat of the ice. Two large lakes persisted for many years in front of the receding ice dam. One, known as Lake Agassiz, covered a large area north of Red Lake and east into St. Louis County, and the other, Lake Duluth, occupied the western part of the Superior basin and covered a narrow strip along the north shore and a wider strip extending into Carlton County, Minn., and along the south shore in Douglas, Bayfield, and Ashland Counties, Wis. Two other lakes of considerable size in Minnesota were drained by the cutting through of land barriers—Lake Aitkin along the Mississippi River in Aitkin County and Lake Upham in Western St. Louis County. Recent botanical evidence indicates that the large sandy area in northwestern Wisconsin, formerly considered to be an outwash plain, may have been, at least in part, a shallow lake (Fassett 1929). The deposits of all of these lake beds are different from those of the surrounding higher lands.

The marked differences in the character of the glacial and fluvio-glacial deposits are due to the differences in action and interaction of the ice, its load, and the water from its melting. Deposits laid down under the ice as ground or overridden moraines, or till plains, have a large proportion of fine material, whereas the drift pushed up or laid down at the edge of the ice and more or

less sorted by water contains coarse sandy and gravelly material characteristic of the sandy moraines. In some places, shallow sheets of water deposited outwash aprons and plains, and in other places, terraces along the swollen streams. Wind had a part in the deposition of some of the sands. Other deposits were laid down in lakes as lake bed formations. Or the presence of lakes caused a sorting of the drift by the waves and the formation of lake beaches. Some of the lakes have been filled in to form peat swamps. Briefly, this is the origin of the surface geological formations which will be used as a basis of classification in a subsequent section.

These same agencies are responsible for the confusing array of hills, ridges, plains, valleys, depressions, swamps, and lakes which characterize the topography of the region. For the most part the slopes are short and gentle or hardly noticeable. In places the sandy moraines are quite hilly and the northeastern rock-outcrop section has numerous short, steep, rocky slopes. The topography is not such, however, as to cause noticeable differences in the tree growth or vegetation because of aspect or exposure. The absolute elevations vary from 602 feet at the surface of Lake Superior to slightly over 2,000 feet on some of the higher hills. This difference also is not sufficient to cause evident distinctions in vegetation or soil. The drainage, to Hudson Bay, to the Gulf of St. Lawrence, and to the Gulf of Mexico, is still immature, as evidenced by the numerous lakes and swamps and the shallowness of most of the stream valleys. This lack of adequate drainage in many areas of varying size is important in its influence on soils, plants, and trees. More complete accounts of the geology and physiography may be found in the work of Leverett (1915) and Leverett and Sardeson (1917).

SOILS

The differences in geological origin of the surface formations are still apparent in the soils of the region, although in time, as the soils mature, these effects will be obscured. Actually, the classification of the soils of the region by the United States Bureau of Soils and the States in cooperation has been largely based on geological origin.[3] The soils of the aspen community were classified according to the soil types described in the Soil Survey reports wherever possible.

[3] By this system soils derived from one source, such as granite or sandstone, or under the influence of one agency, such as alluviation or weathering in situ, or having a certain content of organic matter, such as muck or peat, are classified in a major group called a series. Each series is subdivided, according to the texture or proportion of particles of different sizes, into classes. A single class of any series is called a soil type, which is the unit of classification used in the soil surveys.

More recently, under the influence of the Russian school of soil science, made available in English by Marbut's translation (1927) of Glinka's work, the tendency has been to consider the soil as separate and distinct from the geological formation with which it may be associated. This is indicated by the following definition: "The soil or solum consists of the outer unconsolidated layer of the earth's crust, from a film to several feet in thickness, which differs from the material beneath it in color, structure, texture, physical constitution, chemical composition, biological characteristics, chemical processes, in reaction and in morphology." And again, "the parent material is that from which the soil is derived by outside forces." Many of the characteristics which distinguish different soils one from another may be observed in a soil profile, a vertical section from the surface to the underlying unweathered material. The profile has several layers or horizons parallel to the soil surface which are more or less well-defined in one or more soil properties or characteristics. As a result of the development of these conceptions, the soil type has been redefined as a group of soils uniform in texture of the surface layer of mineral soil, and of uniform profile.

The aspen community was sampled on 54 different soil types. It probably occurs on almost as many more types which did not happen to be represented by any of the plots. Almost all of these types belong to the large regional group of soils of the podsolic soil province, which extends eastward from northern Minnesota and Wisconsin across Michigan and parts of Indiana and Ohio to New York and Maine. These podsolic soils have all developed under the influence of a climate and vegetation of temperate latitude. They have certain characteristics in common. The upper or A horizon has a high content of silica. The iron and aluminum constituents have in part been removed and have accumulated in the underlying B horizon. Some of the iron from the A horizon has been entirely lost in the drainage water. The alkali and alkaline earth compounds have been lost in large part from both A and B horizons. A part of the soil types are true podsols in which the leaching of the A horizon has been sufficiently active to cause a light gray color contrasting with the brown or red of the underlying B horizon. The rest are brown forest soils or transitions between them and the podsols, in which leaching has been less intense and the contrast between A and B horizons is slight or imperceptible to the eye. The numerous soil types represent too fine a degree of subdivision for analysis with the number of plots available. Therefore, for the study of soil-profile groups and relations, the plots were classified into 22 categories on the basis of observable profile characteristics. These were further condensed for certain purposes into 12 and 6 groups, always grouping those which had important characters in common. These groupings are believed to have significance but they do not correspond to any soil groups which have been described in the literature.

Soils develop under the influence of climate and vegetation. Although they change slowly, they are distinctly dynamic and not static in nature. Under certain conditions perceptible changes may take place within a human generation. Under others, changes are apparently very slight in many hundreds of years, and may even be comparable in rate with the changes in climate which have taken place in the 12,000 to 20,000 years since the melting of the glacial ice. Evidence of changes of this last order may be observed in the highly podsolized mature soils in which a gray podsol layer extends to a considerable depth. This development probably took place in large part during the period of cool, moist climate and vegetation of the succession to the Picea-Abies-Betula climax, following the retreat of the ice sheet. Subsequently the sharpness of the podsolic profiles has been dimmed, perhaps during the hypothetical xerothermic period, which was accompanied by invasion from the south and west (Gleason 1922).

On the western edge of the region, the duration of this period was sufficient for the formation of soil profiles with a dark-colored A horizon of mineral soil, high in organic matter from the excess of accumulation over leaching of the decaying roots of the grassland vegetation. Still more recently,

the climate seems to have become again more moist so that the deciduous forest communities are tending to invade the grassland areas and arrest if not reverse the process of prairie soil formation. But the change in climate has not yet been sufficient to cause a further southward advance of the Picea-Abies community. On the contrary, the evidence suggests that the deciduous forest is advancing northward at the expense of the Picea-Abies community.

The significance of this movement in soil development lies in the bearing which it has on the podsolization process. In northern Europe, raw humus is associated with and considered actually to cause podsolization, and the vegetation which is charged with the formation of raw humus is that of the Picea, Pinus, or more nearly arctic communities. Such species as *Vaccinium myrtillus, V. vitis-idaea,*[4] *Calluna* spp., and *Cladonia* spp. are usually mentioned in this connection (Tamm 1920). Here, these species or those most closely related to them are characteristic of the northeastern conifer forest or of the arctic communities and not of the deciduous forest. Furthermore, the associated raw humus has not yet been found in this region if it occurs at all. The conclusion is suggested that the podsol profiles commonly observed in the aspen community are the result of an earlier period of cool, moist climate and northern conifer forest vegetation, and that the podsolization process is not active at the present time. In fact, as indicated by evidence brought forward at the Harvard Forest in Massachusetts (Fisher 1928, Griffith, Hartwell, and Shaw 1930), it seems likely that, under the influence of the deciduous forest and present climate, the soil-forming process tends at present toward the conversion of the podsol to the brown earth profile.

VEGETATIONAL HISTORY

The past history of the chief features of vegetational change just mentioned in connection with changes in climate and soil includes, first, a series of successional stages from herbs through shrubs and forests of Pinus to the climax of Picea-Abies-Betula under a cool moist climate; second, an invasion of prairie and deciduous forest communities during a hypothetical xerothermic period, and, third, the invasion of both prairie and northern conifer forest by the deciduous forest stages leading to the *Acer saccharum*-Tilia climax. The last process is continuing at the present time, if one may come to this conclusion from the prevalence of transitional communities with representations of the species of both Abies-Picea-Betula and *Acer saccharum*-Tilia climaxes in varying proportions. The subordinate arboreal and other plants of the aspen communities sampled provide numerous examples of the early development of the mixture of the two climaxes as well as of each of them separately.

A large part of the area of the aspen community in the region was occupied before human interference by one or the other climax forest, by the

[4] Scientific names used throughout are from Rosendahl and Butters' "Trees and Shrubs of Minnesota" (1928) for the woody plants, and from Gray's Manual (1908) for other plants.

transition between them, or by a subclimax dominated by *Pinus strobus*. *Populus tremuloides* probably occurred as a dominant in limited areas and as an inconspicuous subordinate species in the climax forests wherever accidents or the death of large trees left openings. Logging and fires destroyed or eliminated most or all of the conifers, maple, and basswood. In the growing season following the fire, the bare habitat was densely occupied by a group of pioneer species composed chiefly of those which came from light and wind-borne seed and from the underground parts of the preceding generation. The commonest of this group are *Aralia nudicaulis, Aster macrophyllus, Betula cordifolia, B. papyrifera, Corylus rostrata, Diervilla Lonicera, Epilobium angustifolium, Fragaria virginiana, Populus tremuloides,* and *Solidago* spp. A large number of other species, relics which escaped the fires or those less efficient in their means of propagation, are more or less frequent associates. Among them all the aspen suckers lead in height growth from the first season. If the aspens are not sufficiently abundant to dominate the community after one fire, they are almost certain to do so after the second, third, or fourth fire.

After 10 years or more under the closed aspen canopy, the more mesic and shade-enduring species gradually invade, become established, and maintain themselves or increase in abundance and stature. Certain tree species grow under the aspen and, if undisturbed, form the next stage in the succession when the aspen dies between the ages of 50 and 100 years. The succession may take any one of several different directions depending primarily upon the environmental conditions. Most commonly it proceeds directly to the northeastern deciduous forest climax or to the northeastern conifer climax. On more xeric habitats, it may pass first to the *Pinus strobus* stage or even to a *P. resinosa* stage. On the hydric side, the succession is often to the Fraxinus-Ulmus-*Acer rubrum* stage or to Thuja or sometimes to a mixture of these two. There are groups of subordinate woody and herbaceous species which are more or less characteristically associated with each of these successions. They will be enumerated, classified, and discussed in some detail in a subsequent section. Before this is done it will be desirable to consider the work of others along similar lines.

PREVIOUS WORK

A certain amount of research has been carried out in the United States and Canada and in European countries on the relations between tree growth, soils, and vegetation by foresters and botanists with different points of view and objectives. Only a little of this work has included the interrelations of all three sets of factors, and still less has been concerned with the aspen community. These investigations, however, afford an interesting background, and insofar as they support or contradict the findings in the present study they tend to bring it into sharper relief.

RELATIONS OF VEGETATION, SOILS, AND GROWTH WITHOUT REFERENCE TO ASPEN

A complete review of previous work including descriptions of all studies which might be considered to be related to the subject is not essential. A selection has therefore been made of those which seem most valuable or which are most nearly related to the subject of the present study. Other references to work on specific details will be included at appropriate places in the discussion, even though they may not be mentioned in this section.

From Cajander (1926) and his co-workers in Finland has come one of the most comprehensive expositions of a plant-indicator classification of habitats correlated with forest growth and soil properties, as a basis for the biological and economic evaluation of land productivity and use for forestry and other purposes. Although the categories of this classification go under the appellation of forest types, the words are used in quite a different sense from that usually given them in the United States. In Cajander's words,

> "all those stands are referred to the same forest type, the vegetation of which at or near the time of maturity of the stands is characterized by a more or less identical floristic composition and by an identical ecologico-biological nature, as well as all those stands the vegetation of which differs from that defined above only in those respects which,—being expressions of differences due to age, fellings, etc.,—have to be regarded as merely accidental and ephemeral, or at any rate as only temporary. Permanent differences call forth a new forest type in cases where they are sufficiently well-marked, or a subtype in cases where they are less essential, but nevertheless noticeable."

The types are named after the most representative plant-indicator species in the typical communities but, in their identification, all the associated species of the community are taken into consideration. The communities in Finland are relatively few. They are made up of a small number of species which are surprisingly persistent under a wide variety of cover conditions. In this respect, the plant-indicator types are found to be more permanent than the forest cover, for both birch and Scotch pine, and sometimes also Norway spruce stands, may occur on the same "forest type." In a comprehensive study of growth and yield, including diameter, average and dominant height, and volume both per tree and per unit area, the types were found to be distinct and the differences between types greater than those within types, in all the respects in which growth was measured. It was concluded that the types are well-suited for the classification of soils and of site qualities for forest growth and yield. Table 2, taken from Valmari (1921), gives the essentials of these relationships, those for Myrtillus being taken as 100.

The figures in table 2 are based on averages of more or less variable individual determinations. Recently Aaltonen (1929) has admitted that the variations in the soil properties within the types are too great for satisfactory conclusions as to their relations to forest types and tree growth. The differ-

TABLE 2. COMPARISON OF RELATIVE TREE GROWTH AND SOIL CONSTITUENTS IN IMPORTANT FOREST TYPES, ACCORDING TO VALMARI (1921)

Forest type	Relative current annual increments		Relative amounts in 8-inch surface layer of —	
	Scotch pine, Age 75	Birch, Age 60	*CaO*	*N*
Oxalis-Maianthemum		185	140	223
Oxalis-Myrtillus	115	117	117	137
Myrtillus	100	100	100	100
Vaccinium	83	83	79	71
Calluna	52		54	64
Cladonia	27		36	34

ence in the lime and nitrogen contents of the soils would almost certainly be associated with differences in soil profile types and surface formations if these had been included in the investigations. On the whole, this Finnish work provides strong evidence of a definite relation between plant indicators, tree growth, and soils.

The scheme was tested in the mountains of Germany by Bjorkenheim (1917), who concluded that Cajander's classification was applicable, with minor modifications, in Germany as in Finland. From 100 sample areas in the Picea forests, he found plant indicator types corresponding to different site qualities and average dominant heights as given in table 3.

TABLE 3. TYPE INDICATORS ASSIGNED BY BJORKENHEIM (1917) FOR DIFFERENT HEIGHTS AND SITE QUALITIES

Type indicators	Dominant height	Site quality
	Meters	
Calluna-Cladonia		V
Calamagrostis	15	
Myrtillus	19	IV
Aira	24	III
Oxalis	29	II
Afforested fields		I

An attempt to extend the Finnish scheme to the northern United States and Canada has subsequently been made by Ilvessalo (1929). His observations, chiefly in the forests of *Pinus contorta* in the West and of *Pinus banksiana* in the East, are admittedly insufficient for general conclusions. However, he sets up plant indicator types and finds that, as in Finland, they represent habitats upon which the growth of the forest as measured by the relation of dominant height and age, is, on the average, distinct. In the *Pinus banksiana* forests of Minnesota (Cloquet) and Ontario, the type is called Vaccinium-Gaultheria with probable sub-types, (a) Vaccinium-Myrica and (b) Vaccinium-Rubus-Papilionaceae. Many of the associated species are recorded from several or all of the types and sub-types. Moreover, the successional point of view, the fact that most of the shrubby and herbaceous species of the

forest are changing and will be replaced by others, is entirely ignored. This is a serious defect in a consideration of the two pine communities sampled in North America because both are single-generation pioneer forest stages in succession. The question inevitably comes to mind whether the scheme, at least in its application to our region, is not somewhat idealized, perhaps even to such an extent that its use would be difficult in many, if not a majority, of our forest areas.

The same basic idea of classifying lands for forest purposes by the vegetation and soils appears also in the recent investigations of afforestation in Great Britain by Guillebaud (1930). There the necessity for this basis of classification is acute because the lands have been deforested for years, perhaps centuries. For the same reason, the vegetation and soil types cannot yet be correlated with the growth of the trees. His soils and plant indicator types include grassland with Pteris on brown earth; heath land on podsolized sandy soils, often with shallow peat; and moorland, including the Molinia and Nardus communities on boulder clay and the deeper peats which are subdivided into Juncus peats, Molinia peats, *Eriophorum vaginatum* L. peats, *Scirpus caespitosus* peats, and mixed types containing Calluna. These types are found to be very different in their suitability for drainage and forest planting.

An interesting attempt to devise a soil classification and show its relation to forest types and site qualities has been made in Latvia by Kirstein (1929). The main divisions are based upon the character of the substratum, as marly loam, sandy loam or gravel, sand, and swamp. The first three groups are each subdivided into four according to amount of lime, physical condition, reaction of the mineral soil, and thickness of the humus horizon. The swamp soils are grouped into four categories according to their acidity. Each of the foregoing subgroups is finally classified as to its prevailing moisture content into dry, moist, periodically wet, and wet. Some of the possible categories in this classification are never filled. For example, there are obviously no dry swamps. Nevertheless, the method is relatively simple and is based on a combination of the most reliable and easily determined soil properties.

To a considerable extent, the forest types, characterized by the predominating tree species and the site qualities on a productivity scale of I to V, were found to correspond specifically with these categories. Insofar as this is true, the classification makes it possible to determine the natural forest type and site quality, even in the absence of forest cover, by observation of the soil profile and determination of acidity and lime content. A few of the soil classes, however, represent transitional stages in the forest and are therefore not specific. For example, a moist sandy soil, low in lime and acid in reaction with poor structure and thin humus, may have either Pinus or Picea forest of site quality II or III. Occasional instances of this kind would be almost inevitable in a classification based on the soils. Conversely, the same forest

type and site quality may be found in more than one of the soil categories. Thus, site quality I for Picea-Quercus forest may be on moist, neutral, marly loam with ample lime; or on moist sandy loam, high in lime and neutral in reaction; or on moist sand, high in lime and neutral. Although this investigation did not include the plant indicators, it appears to be quite satisfying for the relations between soils, forest types, and their productivity in a limited region.

A somewhat different line of attack was made in Germany by Barth (1928). He selected areas of the Quercus community representing five different site qualities based on a comparison of average height of stand with yield table values. Profile descriptions and soil samples at three depths were taken and analyzed for texture, water capacity, air capacity, hardness, organic matter, nitrogen, SiO_2, Fe_2O_3, Al_2O_3, CaO, MgO, K_2O, and pH. The soil profiles were distinct from one another in several respects, among which degree of podsolization as indicated by the degree of leaching in the upper horizons and the formation of ortstein in the lower should be mentioned. The conclusions were as follows: In soils of high moisture content, the closest relation to site quality or productivity is found in the air capacity, lime content, and reaction; the height-site qualities of yield tables are only average values and are not always applicable to specific habitats; the associated vegetation serves to indicate changes between adjacent habitats chiefly by changes in the relative abundance of the common species for those particular habitats and the absence or appearance of less common species. Although this study was concerned primarily with soil properties rather than soil types, it has a special interest because it is limited to those changes in environment which may be related to growth within a single forest community, the same limitation that is imposed by confining the present discussion to the aspen community.

In Sweden, vegetation and soil types have been studied and correlated by Tamm and Malmström (1926), although they have not yet introduced the growth or productivity factor into the correlations. The point of view has been the practical one of indicating differences in habitats which correspond to differences in the forest and accordingly require special silvicultural treatment. The other noteworthy feature of the Swedish work in comparison with that of other European countries is the recognition given to the dynamic and changeable character of both vegetation and soil types. In the former respect, the succession after fires has been shown to pass from Betula and Pinus to Picea; in the latter, the time for the development of the podsol profile has been quite definitely established as between 100 and 1,500 years, depending upon the vegetation and environment. Furthermore, Tamm (1920) has shown that the different vegetation types, by means of the humus produced, influence markedly the rate at which leaching and podsolization proceed.

The most recent summary of the soil types and vegetation by Tamm (1930) summarizes the types as follows: The two main divisions are podsols

and brown earths. The latter, limited in Sweden to the southern part, have deciduous forest, and on the moraines chiefly Fagus with the herbaceous plants, Anemone, Hepatica, and Oxalis. The podsols include soils with mull or mild humus and deciduous forest; soils with raw humus without ortstein, having Vaccinium-rich or lichen-rich pine forests; soils with raw humus and with ortstein, having Calluna heath or, in the north, conifer forest; and humus podsol soils, having sphagnum-rich heaths or forests of spruce and also pine and birch of the Dryopteris type. The vegetation classification of Tamm and Malmström (1926) is much more detailed than that of the soil but, lacking the soil equivalents, no useful purpose would be served by reviewing it.

The plant-indicator type idea has been applied to the Danish beech forests by Bornebusch (1931). He distinguishes basic types as the equivalents of the Finnish forest types, which have different soils and cause different flora types within the beech forests. These types are (1) Circaea type, on brown loamy or clayey, high-lime, marl soils with mull and pH, 5.5 to 7.0; (2) Corydalis type, on deep mull soils,—the best sites for beech, which there grows to a height of 30 meters; (3) Mercurialis type, soils more moist and low, good sites for beech; (4) Circaea-Asperula type, somewhat low sites, medium for beech; (5) Primula or Ficaria type, low flat moist sticky soils, poor growth of beech; (6) Anemone-Asperula type, loamy sand and gravelly soils, mull not influenced by limey C horizon, average site for beech; and (7) Oxalis type, degraded brown earth soils with raw humus, gray A_2 horizon and mull of pH 4.0 to 5.5. Additional plant indicators are enumerated for each type but very few of them or of the type species seem to be characteristic exclusively of a single type. *Circaea lutetiana* is listed in 1, 4, and 5, *Anemone nemorosa*, in 2, 3, 4, and 5, Mercurialis, in 2 and 3, Oxalis and Veronica in 4 and 7, and similarly with most of the species. The two interesting things in this study are the lack of specific indicator value of individual species by themselves and the possibility of differentiating useful groups of plant-indicator types with corresponding soil and site-quality differences within a single forest community.

A thorough classification of so-called "forest types" in Russia has been made by Krudener (1927). He defines his forest types as definite plant communities which have developed under given climatic, soil, and underground conditions. Further, the principal soil and geological formations, typical soil and subsoil conditions in relation to soil moisture, aeration, and the character of the organic surface horizon—in connection with the mineral substratum and parent material and in the presence of a definite shrubby and forest community—give definite micro land classes or forest types. His approach to the plant community or forest stand, therefore, is through the environment, climate, and soil. Theoretically, he discusses the different orders of subdivision: First, the climatic and physiographic regions; second, within each, the mineral substrata, whether sandy, loamy, or stony, and their water

regime; third, the soil types, including such categories as plant and plant-mineral layers, black earth, humus carbonate, humus layers of mould, mull, and raw humus, and the alluvial silt and peat deposits with excessive moisture. Actually the "forest type" classification is one of soil types in which hygrometric groups, organic or mineral substrata, soil moisture, aeration, and character of the upper organic horizon are combined with petrographic, physico-mechanical groups into 15 types. The correlation of these types with forest composition is indicated to some degree, but less clearly with site qualities. Thus, although the soil and habitat classification is exceedingly thorough, the resulting categories in many instances are not distinct either with respect to the actual forest cover or to the productivity of any given kind of forest. At the same time some of the soil types include site qualities with ranges as wide as I to III or IV to VI. Again it appears that a classification based on soils does not correspond in its categories to specific forest types and site qualities.

One of the most interesting and complete plans for the classification and correlation of habitats, forest growth, and plant indicators has recently been made available in German by Pogrebnjak (1930). It is based on the work of Alexejew in the Ukraine. The habitat classification is constructed from two features of the soil—the mechanical (petrographic) composition and the depth of the ground water. The former, in effect the chemical fertility of the soil, is divided into six degrees to form graduations along a horizontal scale from low through rich to "excessive" (in alkali soils). Similarly, different levels of the ground water correspond to six graduations of a vertical scale from very deep at one extreme to very shallow or surficial at the other. The latter scale corresponds closely to the range from xeric to hydric. The two scales are combined as coordinates in a diagram on which the distributions of the species of trees and plant indicators and of the site qualities of the forest stands are outlined to form what is termed an ecofigure. Each species or productivity class thus forms a closed area on the diagram, the perimeter indicating the limits of distribution as determined by soil fertility and moisture, and the center the optimum for that species or class. In this way the inter-relations of species or communities and growth rates may be compared visually with one another in respect to their responses to fertility and moisture which define the habitat categories. The scheme obviously requires a thorough knowledge of certain key trees and plants in relation to their habitats for its initial construction but, once constructed, it effectively coordinates habitats, plant indicators, and forest productivity.

In the United States, the relations between soil and forest growth have been studied by Haig (1929) and (in Connecticut) by Morgan (1930). They both used the site index of Norway pine plantations as the measure of soil productivity and have correlated that with certain soil properties, types, and classes. Some preliminary work with the natural mixed hardwood forests and the soil types as mapped by the Bureau of Soils proved disappointing. Sub-

sequently Haig found significant correlation indices between the Norway pine site index and soil conditions, as follows: Colloidal content of the A horizon, 0.52; colloidal content, A and B horizons, 0.55; silt plus clay, A horizon, 0.58; and colloidal content plus organic matter plus reaction, A horizon, 0.65. Correlation with soil class was 0.70, and with soil type 0.80. Sufficient data were not available for an adequate investigation of the soil type correlation but it is suggestive that the soil type, which integrates all of the soil factors, seemed to be more closely related to tree growth than any of the individual soil properties or lesser combinations of properties.

Additional work is reported by Morgan to the effect that the moisture equivalents of the A horizon show a somewhat better correlation with site index than the texture, that no definite correlation could be established with the soil reaction, and that a suggested correlation was found with the replaceable calcium of the A horizon. Low transformation of nitrogen into ammonia and nitrates was associated with low site index. High site indices occurred on soils which showed a tendency to form a raw humus layer, although in general the soils with active earthworm mull were slightly superior.

The plant indicator concept, in relation to soil types, agricultural productivity, areas for afforestation, and forest communities, has already a considerable literature which is well known. The works of Hilgard (1906), Shantz (1911), Korstian (1919), and Clements (1920) do not require detailed review. Korstian called attention specifically to the probable value of plant indicators of different site qualities for the growth of trees and cited the example of *Pinus ponderosa* in New Mexico where site I with mesic species produced 64 percent more increment than site II to which certain xeric species were limited.

Recently Holman (1929) in Alberta has enumerated the ground vegetation characteristic of each of three site qualities as determined from the rate of growth in pure forest sample plots. Brief notes of the humus conditions do not sufficiently characterize the soils. Many of the plants, however, belong to the same genera as those to be presented hereafter and are therefore of some interest. They are tabulated below in parallel columns. Site I is the best and site III the poorest.

SITE I	SITE II	SITE III
Actaea	Alnus	*Antennaria microphylla*
Alnus	Fragaria	Arctostaphylos
Coptidium	Ledum	*Hedysarum sulphurescens*
Corylus	Mertensia	*Juniperus siberica*
Heracleum	Moneses	*Sabina horizontalis*
Mitella nuda	Petasites	*Zygadenus elegans*
Oxalis	Pyrola	
Pteridophyta	Rosa	
Ribes	Salix (dwarf)	
Salix	Shepherdia	
Smilacina	*Vaccinium* spp.	
Viola	*Vaccinium vitis-idaea*	

The relation of natural vegetation to soil types and their acidity has been investigated for six soil types in Pennsylvania by Kelly (1922). The soil types, their pH and the characteristic plants, including only those also found in this study, are given below.

SOIL TYPE	CHARACTERISTIC PLANTS
Hagerstown loam (pH 7.2)	*Quercus alba, Fraxinus americana, Corylus americana, Celastrus scandens, Equisetum hyemale, Asarum canadense, Aquilegia canadensis, Mitella diphylla.*
Manor Valley loam (pH 7.2)	*Ostrya virginiana, Prunus pennsylvanica, Fraxinus pennsylvanica lanceolata, Osmunda cinnamomea, Lycopodium annotinum, Trientalis americana.*
Conowingo loam (pH 7.1)	*Acer rubrum, Andropogon scoparius.*
Chester loam (pH 7.0)	*Quercus rubra, Ulmus americana, Prunus americana, Fraxinus americana, Amelanchier canadensis, Smilax herbacea, Iris versicolor.*
Manor loam (pH 6.6)	*Carya cordiformis, Betula lenta, Viburnum acerifolium, Pteris aquilina, Viola pubescens.*
Dekalb loam (pH 6.2)	*Amelanchier oblongifolia, Symphoricarpos, Iris versicolor.*
Manor stony loam (pH 5.7)	*Epigaea repens.*

Many other species, occurring on most or all of the soil types, were not considered characteristic. The differences between soil types are not striking and it may even be questioned whether the characteristic species would have continued to be characteristic, if a larger number of sample areas of each soil type had been examined.

After studying in considerable detail the properties of four soil types on the Mont Alto State Forest in Pennsylvania, Auten (1930) concluded that volume growth of wood was independent of soil texture and had no perceptible relation to total nitrogen, phosphorus, or calcium or to the microorganisms present. Aspect and exposure, in their influence on soil moisture, were found to cause differences in floristic composition and as much as 100 percent difference in volume increment as between cool moist and dry exposed sites "on the same soil type." It seems possible that a difference in soil type may have existed in situations of such contrasting character. However that may be, the change in volume growth with difference in habitat is clear, and in addition there is a difference, not in the plant indicators within a community, but in the tree dominants themselves.

The phytometer method has been much used in ecological investigations by Clements and Goldsmith (1924), Clements, Weaver, and Hanson (1929), and others. It has been proposed for, and would seem to be well suited to, the study of plant growth as a measure of habitat; but for some reason it has

been little used in the measurement of soil productivity, unless the measurements of growth in forest communities be considered as examples of free phytometers. In that sense, the plots of the aspen community may be considered as phytometers.

ASPEN GROWTH, ASSOCIATED VEGETATION, AND HABITATS

Only a small proportion of the comparatively little work that has been done in the aspen community covers the relation between aspen growth, associated vegetation, and habitat. In northern Europe, Schotte (1916-17) found *Populus tremula* on two distinct sites, one producing 200 and the other 150 cubic meters at 50 years. They were also distinct in respect to vegetation and soil. Eklund and Wennmark (1925), supplementing Schotte's work in Sweden, found that the height of the aspen appeared to be specially affected by the character of the soil, which they considered to be the dominant factor. At 50 years on site quality I the height of the aspen was 68 feet and on site II, 56 feet, with corresponding differences in volume growth.

In the United States, a study of aspen in New England by Weigle and Frothingham (1911) showed marked differences in growth on different sites. The heights at 50 years were 75 feet on site I, 65 feet on site II and 50 feet on site III, but these sites were not described as to their soils or associated vegetation. In the Central Rocky Mountain region, Baker (1925) distinguished 5 sites for aspen on the basis of the height of dominant trees at 50 years and briefly characterized the habitat of each site quality as follows: Site 1, height 57 feet, on moist flats with deep, rather heavy soil; site 2, height 48 feet, less well watered than 1 and more often on slopes; site 3, height 37 feet, similar topography to 2, but below the optimum altitudinal zone for aspen; site 4, height 30 feet, at the lower limits of the type and on south slopes at higher elevations; site 5, aspen of unmerchantable thicket type, on poor soils of south and west slopes, particularly above the zone of best development. Baker notes that there is extremely close correlation between height and annual volume increment as criteria of site, and the foregoing habitat descriptions indicate relationship between growth and habitat, although not in terms directly comparable with any of the soil classifications used in the present study.

A detailed frequency analysis of the vegetation of the aspen community in northern Lower Michigan has been made by Gates (1930). He classifies the species in three categories, pineland, hardwood, and lowland, which correspond to different habitats, namely, dry sandy upland, moderately moist loamy upland, and moist lowland, but these habitat categories are rather broad and no correlation is made with the growth of the aspen. His analysis shows, however, that the habitats may be distinguished by the composition and frequency of occurrence of the associated species in the aspen community.

Earlier, in the same vicinity, the associated species of the aspen community

were studied in connection with the theory of species and area by Gleason (1925). After computing frequencies for the different species on different combinations of quadrats, he concluded that "environmental differences in the aspen association, while observable, are not of sufficient magnitude to affect the distribution of the species," and again, "within the limits of a single plant association, the environment, while possibly presenting observable differences, is essentially homogeneous for each species." His quadrats, however, were on level terrain in a soil of almost pure sand in which repeated tests of soil acidity failed to show any variation. A wider sampling of the aspen community might have modified these conclusions. It will be interesting to compare these statements with findings in the later section on plant indicators in relation to habitat.

The growth of aspen, including the preparation of site-index curves, has been analyzed in considerable detail by Kittredge and Gevorkiantz (1929), largely on the basis of the data of the present study, but with little consideration of habitat and plant-indicator relations. There is no reason to review those findings, since much more complete and critical analyses of the same material are made in the following sections.

ANALYSIS OF GROWTH RATE

Possible Measures of Tree Growth

Features which, observed over a known period of time, provide a measure of tree growth rate include dry weight, leaf area, crown dimensions or volume, stem dimensions or volume, and heights of all or of the dominant trees.

Dry weight is ordinarily considered, and logically so, to give the best measure of growth, because it includes all of the dry matter produced by the plant reduced to a standard moisture content. Total leaf area gave results corresponding closely to those by dry weight in the work on competition by Clements, Weaver, and Hanson (1929). But neither of these features provides a measure of growth for trees of greater bulk than 15-year-old trees. Crown diameter and length may be measured rather closely and may be combined to obtain crown volume, which supposedly would give values comparable to léaf area. But this measure becomes almost prohibitive when 20 or more trees on each of 277 plots are concerned. Moreover it would be particularly susceptible to variation with differences in density of the stands, and thus differences due to soil productivity would be obscured.

Lengths of the stems or total heights and diameters at 4½ feet above ground are readily measured on sample trees and when combined with a form factor express quite accurately the volumes of the stems. This is the measure of volume and growth commonly used by foresters in all countries. Although its use is dictated in part by reasons connected with utilization of the wood, there is no reason to believe that, for any given species of relatively uniform crown development like aspen, it is not at least closely correlated with dry

weight and leaf area. Stem diameters and volumes, however, are also subject to wide variations with differences in density.

Finally the heights of the taller or dominant trees, which receive full light from above and some from the sides, may be averaged to provide a measure of growth. Since height growth in well-stocked stands, or stands in which the density factor is relatively constant, has been shown by Gevorkiantz and Zon (1930) to be a linear function of volume growth, this characteristic may be used in place of volume growth. It has the advantage, as compared with volume growth, that it is influenced less by changes in density and this influence is minimized if the heights are limited to those of the dominant trees. It has frequently been observed in height measurements of forest trees of the same age that those growing in the open and those in very dense groups are shorter than those in stands of moderate to well-stocked density. The same thing is proved in the controlled experiments of Clements, Weaver, and Hanson (1929) with Helianthus, Xanthium, Triticum, and Andropogon. They grew cultures with the plants spaced uniformly at intervals of 2, 4, 8, 16, 32, and 64 inches. Heights reached a maximum with the 4- or 8-inch spacings and decreased somewhat as the densities were either greater or less than these. Thus, although height growth is not a reliable measure of productivity in either extremely dense or extremely open stands, it probably is more reliable than any of the other measures over quite a range of intermediate densities, such as are represented by most of the plots in this study. Stem volume growth and height growth of dominant trees have both been used in this study and further comparisons of them will accordingly be made.

STEM VOLUME GROWTH PER UNIT AREA

The components of stem volume as a measure of growth rate are diameter, height, form, age, and density. From the direct measurements of diameters and heights of sample trees, curves of height over diameter were drawn for each plot and the values read from these curves were used for the heights of the trees for which only diameter measurements were available. The volumes were then read from volume tables based on diameter and height, already available. The preparation of the volume tables makes allowance for the factor of form of the stems (volume $=$ diameter^2 $\times$ height $\times$ form factor) insofar as it varies with diameter; height and further variations due to age or density within any given diameter and height class are believed to be negligible or at least well within the limits of error to which some of the other data are subject. Density, expressed as number of aspen trees per acre, cannot be ignored when using volume growth as a measure of productivity. Accordingly it seemed essential to limit the application of the volume growth criterion to a group of plots in which the density was relatively uniform. This was done by separating the well-stocked from the understocked and overstocked plots and using only the well-stocked in the measurement of productivity. This separa-

tion on the basis of density appears somewhat involved where plots of different ages growing on different soils are concerned because these are themselves factors affecting density.

As a first step, the values of number of trees per acre were plotted over mean diameter for each of the 248 plots (fig. 2). It may be seen that the number of trees per acre decreases very rapidly as the mean diameter increases from 1 to 3 inches, more gradually from 4 to 9 inches, and very slowly from 9 to 15 inches. The two coordinate axes tend to form asymptotes to the two

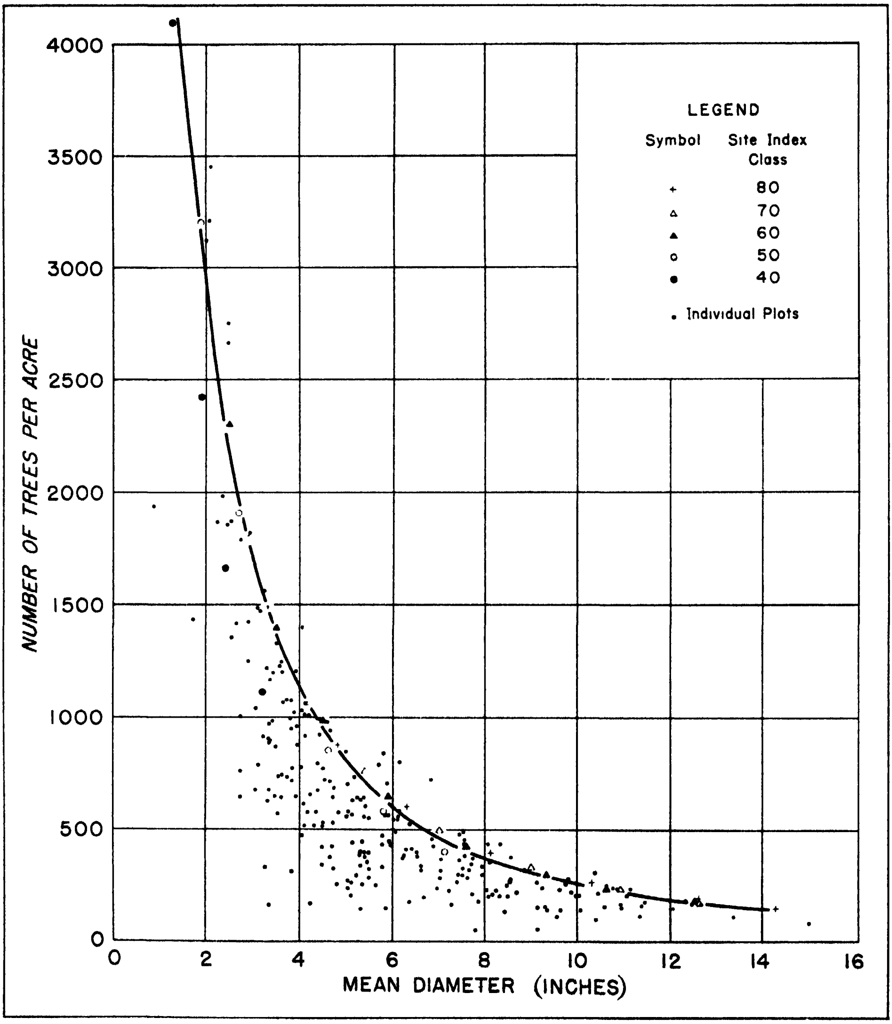

FIG. 2. Relation of number of trees per acre to mean diameter. The dots represent plotted values for each of 248 plots; the symbols represent the smoothed averages of age and site-index classes, as obtained from 103 well-stocked plots.

ends of the trend, and this, with the general form, suggests that it may be represented by a hyperbola. As a preliminary test of this possibility, the average figures for numbers of trees per acre and mean diameter derived from the 103 well-stocked plots, previously segregated by means of the relation of basal area[5] to age and site index (Kittredge and Gevorkiantz 1929), were also plotted and a smooth curve drawn through them. The trend of the points is strongly and closely defined. When values read from this curve were then plotted on logarithmic paper, they formed a straight line (fig. 3, line F–F), thus confirming the suggestion that the relationship could be represented by a hyperbola.

It may be observed that the excellent alinement of these points was obtained in spite of the fact that they represented different site-index groups and different ages. This confirms the conclusion of Gevorkiantz and Zon (1930), who refer to the idea of Russian workers, that the relation of number of trees per acre to average diameter is independent of age and site quality. This relation is reasonable from biological considerations. Assuming a specified area of ground, its full productive capacity may be utilized either by a small number of large trees or by a large number of small trees, provided the trees are growing in pure, even-aged stands. Any increase in the size of the trees due to greater age is associated with mortality of the weaker individuals and reduction in the number of trees on the area. Similarly, on a good site as compared with a poor site, the individual trees grow larger but the number of them which can survive is not as great. If the stand is very dense at the start, the diameter growth of the trees will be retarded but their number per unit area is greater. The separation of cause and effect in this relation is not always easy, but its reciprocal nature and its independence of age and site quality, which are expressed in the mean diameter, seem logical.

Finally, the values of average diameter and number of trees per acre for each plot were also plotted on figure 3, separating those for the well-stocked plots from the others. The points representing well-stocked plots are concentrated along the trend line while most of the others fall considerably below it. This relationship, therefore, seems to offer a check or alternative method for the division of stands on the basis of stocking or normality. Deviations to the left or below the straight line trend formed by the upper band of points on the logarithmic paper would result when a stand had any combination of subnormal number of trees per unit area with subnormal diameters. Such a combination might be due to competition of other species in the stand, or to suppression of some or all of the aspens by larger trees of other kinds, or to early suppression of the aspen by trees which were subsequently cut. Stands which had been subject to any of these influences would evidently require careful scrutiny before they could be considered reliable as indicators of soil

[5] Basal area $= \Sigma(\frac{\pi}{4}d^2)$ per acre.

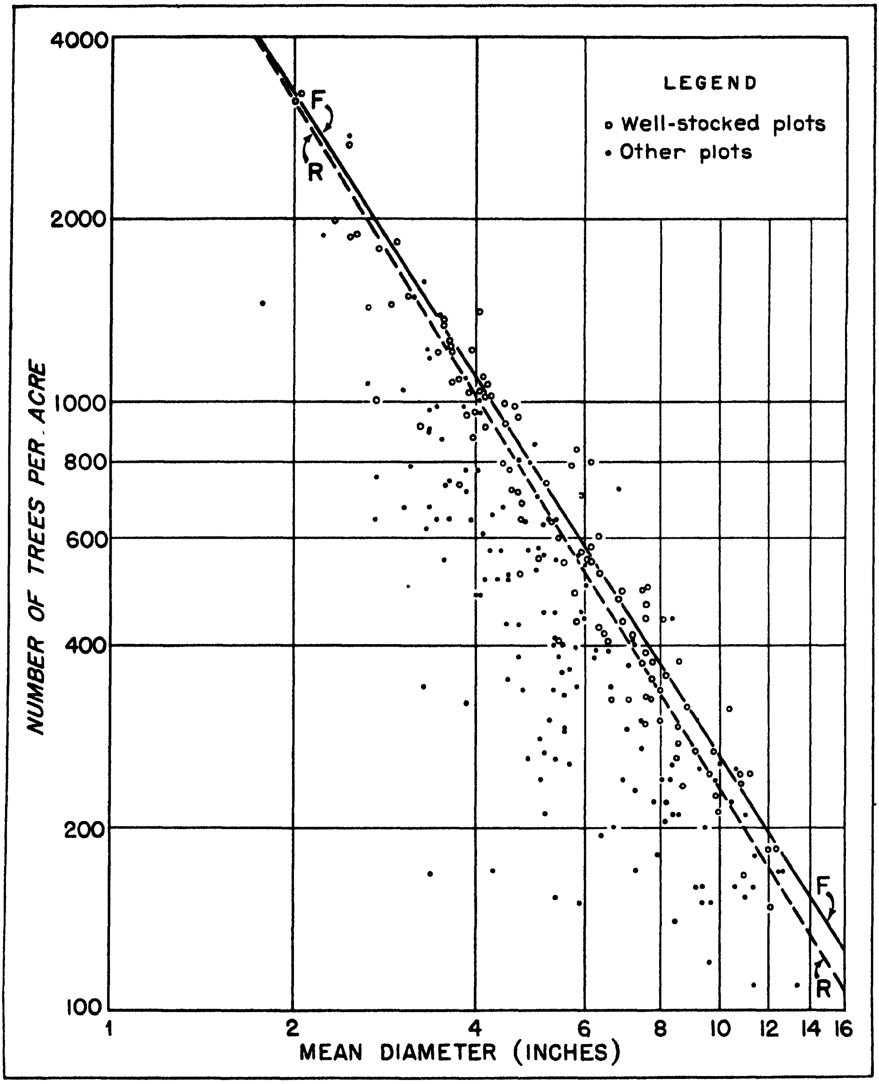

FIG. 3. Determination of hyperbolic relationship of number of trees per acre and mean diameter. Line *F–F* connects smoothed average values plotted from the curve in figure 2. Line *R–R* is a regression line plotted from the formula $\log D = 2.44 - 0.61 \log n$.

qualities. Deviations on the side of the curve toward the origin would also result (and probably more commonly) when insufficient seed or parent roots at the time of establishment caused the number of trees per acre to be subnormal. In such cases, even though diameters would tend to be abnormally large, a young stand with few trees per acre would not immediately put on diameter increment sufficient to maintain the normal relationship between

diameter and number of trees per acre. For example, suppose that only 200 trees per acre appear after a fire. The normal diameter for a stand of 200 trees per acre is about 11 inches. Evidently, however, these 200 trees cannot possibly attain diameters of 11 inches for 40 or 50 years. During the intervening period, the stand will be judged subnormal by the criterion of *diameter-number of trees per acre.*

In order to establish a standard of normality in respect to the relation between diameter and number of trees per acre, a straight line was fitted to the logarithms of the values of the 103 plots which were judged to be well-stocked by field observations. The general equation of a hyperbola when there is no constant term is $y = ax^{-b}$ or for these data, $D = an^{-b}$. In logarithmic form this becomes, $\log D = \log a - b \log n$, which is the equation of a straight line on logarithmic paper. The two normal equations by the method of least squares then are,

$$\Sigma \log D = N \log a - b\, \Sigma(\log n)$$
$$\Sigma(\log n)\ (\log D) = \log a\, \Sigma(\log n) - b\, \Sigma(\log n)^2.$$

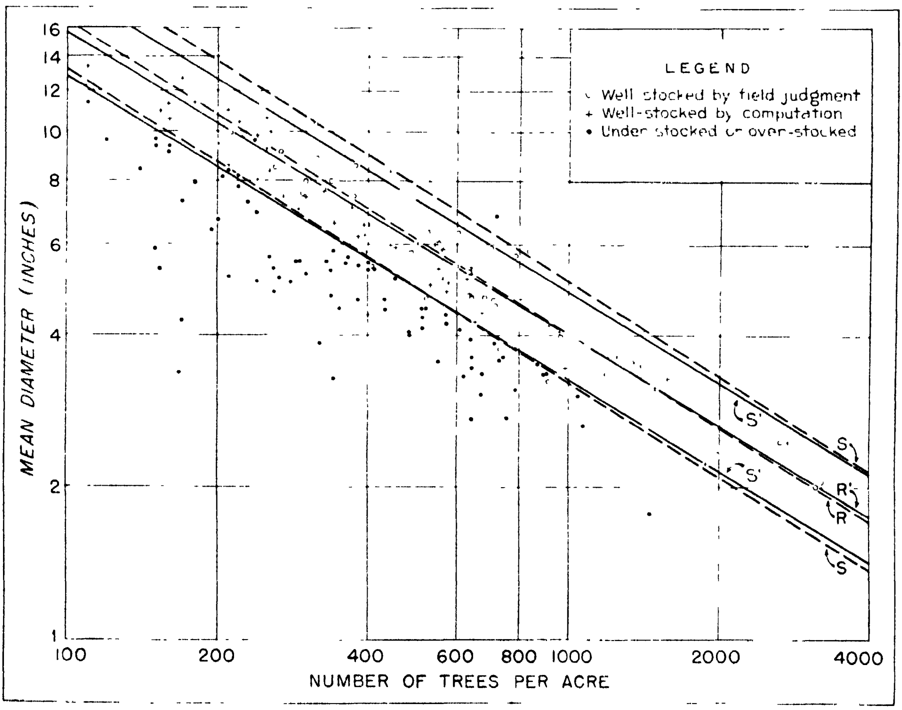

FIG. 4. Plotted points from figure 3, with line *R–R*. *S–S* is a band defining the limits of twice the standard deviation about the line *R–R*. The line *R'–R'* is a new regression line, $\log D = 2.38 - 0.59 \log n$, calculated by the inclusion of the 58 plots, originally recorded as poorly stocked, that lie within the band *S–S*. *S'–S'* is the new band based on *R'–R'*. Nine plots included in *S–S* are rejected by *S'–S'*. (Although the variables as presented in figure 3 are interchanged, the equations in every case represent the regression of log diameter on log number of trees.)

Computing, summing, and substituting the values in these two equations, they become,

$$75.7039 = 103 \log a - 287.4251\ b$$
$$205.6132 = 287.4251 \log a - 811.3025\ b.$$

A solution of these two simultaneous equations gives $b = 0.6105$ and $\log a = 2.4386$. These two values substituted in the original logarithmic equation give

$$\log D = 2.4386 - 0.6105 \log n$$

which is the equation of the regression line of $\log D$ on $\log n$.

This line is plotted in both figures 3 and 4 as R–R and obviously fits the trend of the 103 well-stocked plots. Although it does not coincide with the line previously plotted, derived from the relation between basal area and age for the same plots, the two diverge so slightly that either one might be used as a criterion of normality of stocking. The relation between diameter and number of trees per acre is much easier to obtain, since it involves only one set of measurements and counts and avoids the computation of basal areas and the determination of age.

The standard deviation (S) about the line of regression was obtained from the relation—

$$r = b_{\log D \log n}\left(\frac{\sigma_{\log n}}{\sigma_{\log D}}\right),$$

where

$$\sigma_{\log n} = \sqrt{\frac{\Sigma(\log n)^2}{N} - M^2_{\log n}} = \pm\ 0.2996$$

and

$$\sigma_{\log D} = \sqrt{\frac{\Sigma(\log D)^2}{N} - M^2_{\log D}} = \pm\ 0.1897$$

then

$$S_{\log D} = \sigma_{\log D}\sqrt{1 - r^2}.$$

If, thus,

$$r = 0.964$$

and

$$S_{\log D} = \pm\ 0.0504,$$

then, $2S = \pm\ 0.1008$. This may be interpreted to mean that, in 95 cases out of 100, another well-stocked aspen plot selected from the same range of environmental conditions would, with respect to its relation between average diameter and number of trees per acre, lie within 0.1008 logarithmic units of diameter above or below the regression line. The two lines representing this range are also plotted on figure 4 forming the band S–S. It may be observed

that, of the 103 well-stocked plots on which the calculations were based, only 7 lie outside this band, 2 above and 5 below, or 96 out of 103 lie within, as compared with the theoretical 95 out of 100.

In addition, 58 of the plots designated in the field as not well-stocked lie within this band. If the 103 plots were insufficient to serve as a basis for the band, these additional plots could be included to make up the deficiency. It may well be questioned, however, how much they would actually modify the band's slope or width.

Certainly, continued repetitions of the process of rejection and recomputation would gradually cause the narrowing of the band until only those values remained which lie on the regression line and would therefore be absurd. Only one repetition with the additional plots was made in this case. For this purpose, all the plots lying within twice the standard deviation about the regression line were used to recalculate a new regression line and new band. With $N = 161$, the formulae are identical with those previously used. The values obtained are,

$$b_{\log D \log n} = 0.5913$$
$$\log a = 2.3762$$

and the regression equation is

$$\log D = 2.3762 - 0.5913 \log n$$
$$\sigma_{\log n} = \pm 0.3105$$
$$\sigma_{\log D} = \pm 0.1888$$
$$r = 0.973$$
$$S_{\log D} = \pm 0.0435$$

and

$$2S_{\log D} = \pm 0.0870$$

This line and its band are plotted in figure 4 as R'–R' and S'–S'. This line is slightly lower and has a little less slope than the first line and the band represented by $2S$ is narrower, the lower limit nearly coinciding with the former position and the upper limit somewhat lower throughout its length. Thus one additional plot below and eight above are rejected as being understocked and overstocked respectively. The remaining 152 plots will be considered normal in respect to the relation between diameter and number of trees per acre in any analysis where it seems essential to have uniformity in these characteristics.

THE AGE OR TIME FACTOR

In order to use the volumes or heights of plots of different ages as a measure of the habitat differences, it is obviously necessary to eliminate or hold constant the age variable. This may be done conveniently by the process of anamorphosis in the same way that Bruce (1923) has suggested its use in the

elimination of age in the preparation of a site-index scale based on dominant height. First the volumes of the 161 well-stocked plots are plotted over age in figure 5. As the trend is evidently not far from linear, the regression line

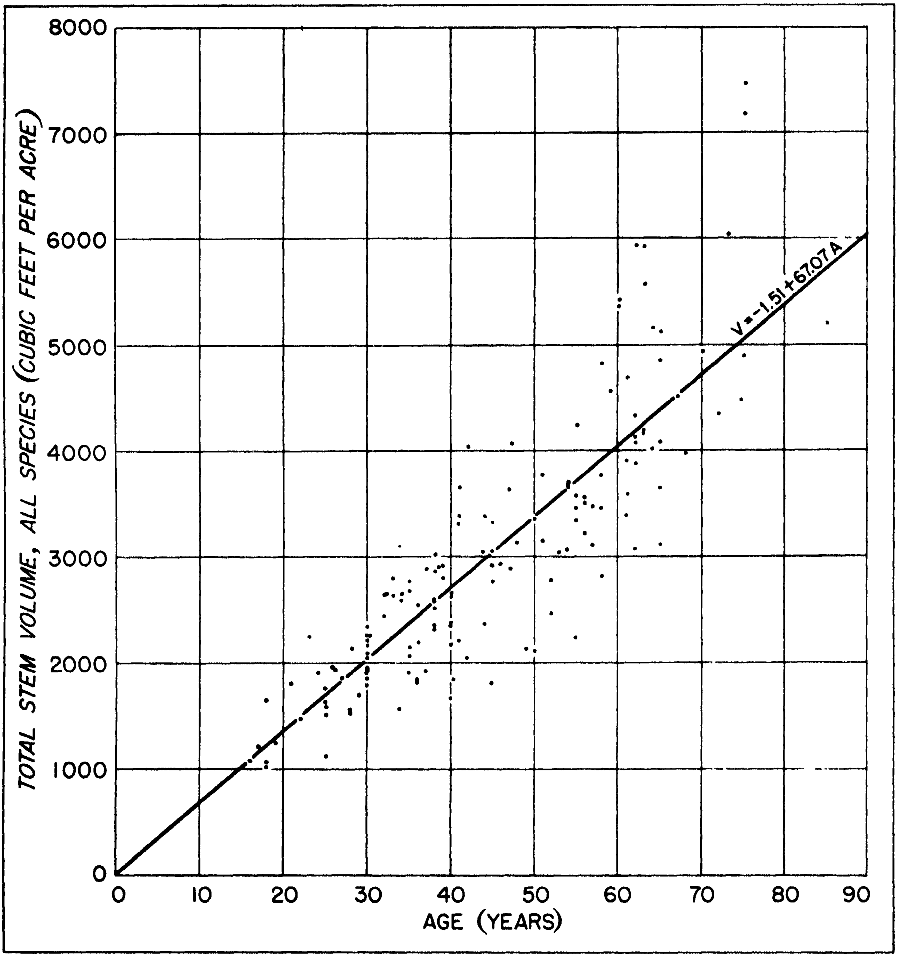

FIG. 5. Relation of volume to age in well-stocked stands.

of volume on age is fitted by the method of least squares. The equation of the line is: $v = a + bA$ when $v =$ volume and $A =$ age. The normal equations then are $\Sigma v = Na + b\ \Sigma A$, and $\Sigma vA = a\ \Sigma A + b\ \Sigma A^2$. Substituting the values, these become,

$$480{,}871 = 161a + 7{,}173b$$
$$23{,}994{,}306 = 7{,}173a + 357{,}751b.$$

Solve the two simultaneous equations, $b_{vA} = 67.073$ and $a = -1.51$, and the regression equation becomes $v = -1.51 + 67.07A$, or the straight

line plotted in figure 5 with its origin close to zero. The volume index is shown in figure 6, where the volume at 50 years is taken as a common denominator. The volume index for any plot is obtained by locating it in this

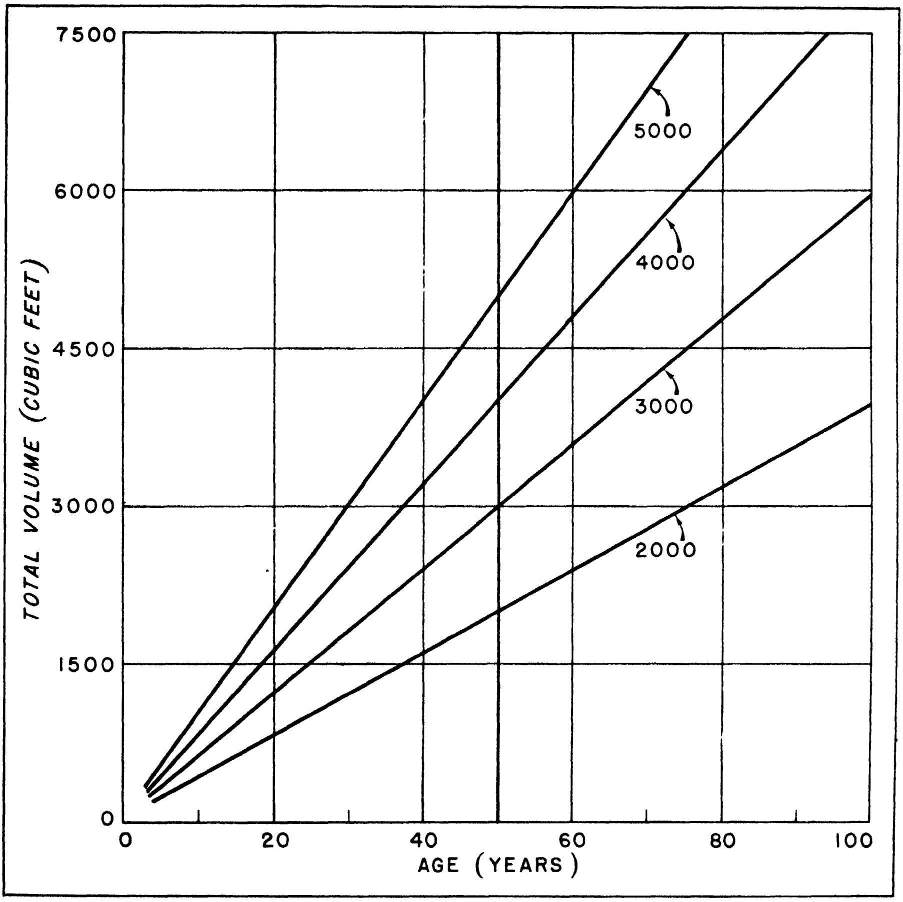

FIG. 6. Volume index for aspen, based on relation of volume to age in 161 well-stocked stands.

new set of coordinates, according to its volume and age, extending the line from the origin through this point to its intersection with the 50-year abscissa, and reading the volume index corresponding to this intersection on the volume scale at the left. Thus every plot of whatever age is expressed in terms of the volume which it would have if it were just 50 years old, and the age variable is held constant. The pencil of lines in figure 6 are those for the even thousand volume indices.

SITE INDEX FOR ASPEN

A series of site-index curves for aspen had previously been prepared by the same process of anamorphosis just outlined for the volume index. These

curves, with an explanation of their use, are available in the publication by Kittredge and Gevorkiantz (1929). For convenience of reference in the present study, they are reproduced in figure 7. They differ from the volume

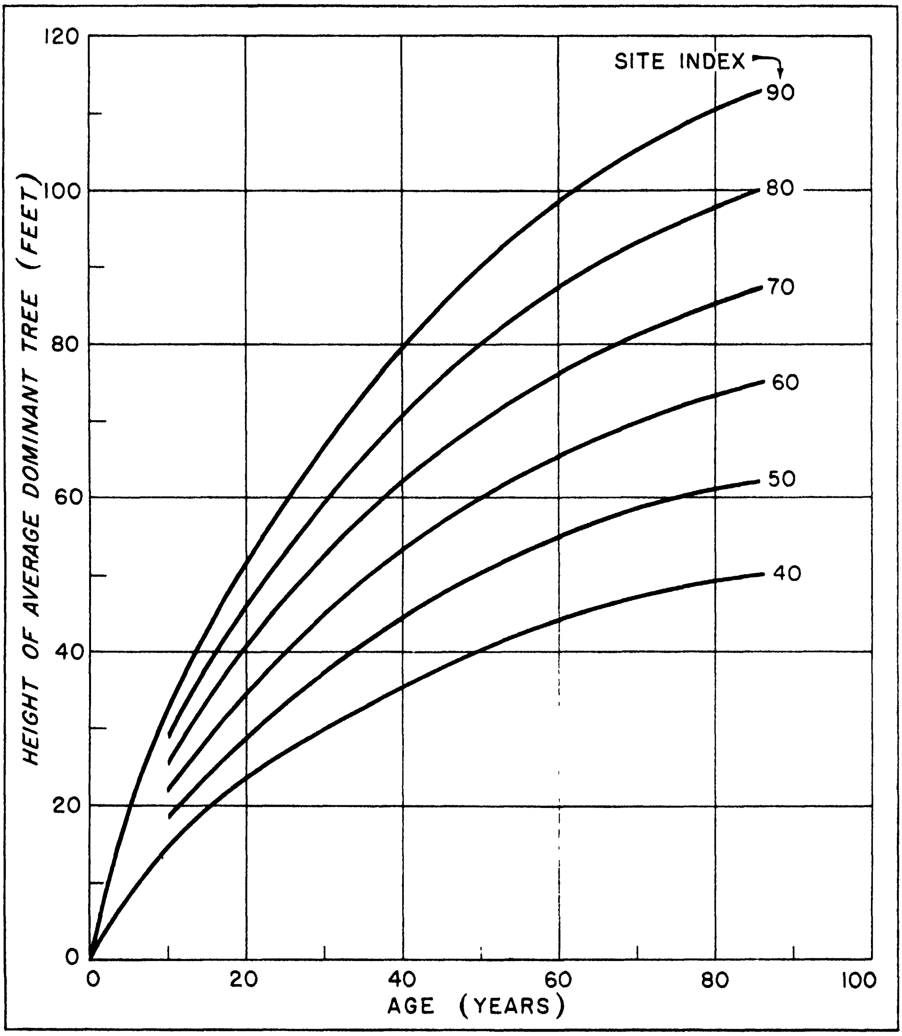

FIG. 7. Site index curves for aspen. (From Kittredge and Gevorkiantz 1929).

index graph in that average dominant height replaces volume and the relationship between height and age is represented by a curve better than by a straight line. The site indices for each plot—in reality dominant height indices—were obtained from these curves, thus providing a second measure of the habitats based on the growth of aspen.

COMPARISON OF VOLUME INDEX AND SITE INDEX

Something may be learned about these two series of measures by studying their variability. For the volume index series, the standard deviation of the 151 plots may be computed from the relation, $\sigma = \sqrt{\frac{\Sigma I^2}{N} - M_I^2} = 669.4$ when $N = 151$ and the mean, $M_I = 3{,}394$. If now, the standard deviation is expressed as a percentage of the mean, a measure of the variability within the series is obtained which is known as the coefficient of variation. In symbols, $V = \frac{100\sigma}{M_I} = 19.8$ percent. This may be interpreted by the statement that 68 percent of the individual volume indices of the well-stocked plots lie within a range of 19.8 percent more or less than the mean.

Similarly, for the site-index series, where $N = 230$ and the mean $M_I = 62.5$, then $\sigma = 7.75$, and the coefficient of variation $V = 12.4$ percent. In other words, 68 percent of the individual site indices based on dominant height lie within a range of 12.4 percent more or less than the mean. The site-index series includes the understocked and overstocked plots which were rejected in the volume-index series. This would tend to increase the variability of the site-index series, and yet in spite of this tendency, the coefficient of variation is only 63 percent as large as that of the volume-index series. The comparison of the two series of measures indicates that the site-index is distinctly less variable than the volume-index. Partly for this reason and partly because the site index is less subject to the disturbing influence of variations in density and can, therefore, be used for all the plots including understocked and overstocked, it will be used as the standard measure in relating aspen growth to habitat and plant-indicator groups. A further comparison of the two growth measures will be made in the correlations with soil groups.

ANALYSIS OF HABITATS

Beause the climate of the region and the local atmospheric variations within a single community are relatively uniform, and because such climatic differences as may exist are reflected in the soil, the habitat classifications are based upon the soils. Five different groupings of soils are made on the following bases: (1) Soil class or texture; (2) geological surface formation; (3) combination of soil class and surface formation; (4) soil profiles; and (5) soil types. A differentiation between the red and gray drift is made in the first three groupings. The groups will be discussed in the order enumerated above.

SOIL CLASS OR TEXTURE GROUPS

The habitat data were first classified into eight soil classes. Beginning with the coarsest, these classes are defined in terms of the component soil separates as follows:

Sand, more than 20 percent medium sand or coarser, less than 20 percent silt plus clay.

Fine sand, less than 20 percent medium sand or coarser, less than 20 percent silt plus clay.

Sandy loam, more than 20 percent medium sand or coarser, between 20 and 50 percent silt and clay.

Fine sandy loam, less than 20 percent medium sand or coarser, between 20 and 50 percent silt and clay.

Loam, less than 55 percent silt, more than 50 percent silt and clay.

Silt loam, more than 55 percent silt, less than 25 percent clay.

Clay loam and clay, less than 55 percent silt, more than 60 percent silt plus clay.

Peat, more than 50 percent organic matter.

Directly or indirectly the texture of soils affects to an important extent their complex relationships to plants. The proportions of the different separates and particularly of the finer fractions, the silt and clay and its included colloids, largely determine the water relations, the aeration, the chemical transformations and the abundance and activity of the soil organisms. In respect to the aspen community in this region, the circulation and availability of soil moisture and its reciprocal relation to aeration give a large part of their significance to the soil classes. The range of moisture contents of the different classes at the moisture equivalent (probably not far from the optimum for plants) and at the echard or wilting coefficient below which the moisture is nonavailable for growth, are shown below in tabular form. The moisture equivalents were compiled from Briggs and Shantz (1912), Middleton (1920), and others, and were converted to wilting coefficients by multiplying by the factor 0.54 as suggested by Briggs and Shantz and modified by Alway (1916) (table 4).

TABLE 4. WILTING COEFFICIENTS FOR SOIL CLASSES AS DERIVED FROM MOISTURE EQUIVALENTS

Soil Class	Moisture equivalent	Wilting coefficient
Sand	2 - 7	1 - 4
Fine sand	4 - 12	2 - 7
Sandy loam	8 - 19	4 - 10
Fine sandy loam	10 - 28	5 - 15
Loam	13 - 29	7 - 16
Silt loam	18 - 33	10 - 18
Clay loam and clay	21 - 41	11 - 22

The overlapping between the moisture "constants" of different classes is at once evident and suggests that plant responses to the different classes will not always be distinct. Furthermore, although the plants of generally mesic communities like aspen more often suffer from lack of moisture in the soils of low wilting coefficient, it is actually the presence of moisture above the

echard that is available and enables them to grow. The difference between total moisture content and wilting coefficient does not necessarily vary with the wilting coefficients. In other words, a plant may wilt in a silt loam soil with 10 percent moisture when it would grow well in a sandy loam soil with only 8 percent. One of the limitations to the establishment of the aspen community is apparently associated with a texture class. The aspen is only rarely found on the dry outwash sands which represent the least moisture-retentive texture class in the region. However, this limitation is a matter only in part of the surface layer and in part also of the subsoil and glacial formation.

The soil classes are based on the texture of the upper 8 inches of soil, and in this fact sufficient reason may be found to explain some discrepancies in the correlation of soil classes with plant growth. Most of the trees and woody plants, after their juvenile stages, have root systems extending considerably deeper than 8 inches. In these lower soil layers, the presence of a layer of heavier texture or the proximity of ground water may quite reverse the expectation as to growth judged from the soil class exclusively. Obviously the growth of aspen and the floristic composition of the community will not be the same on a fine sand along the margin of a swamp as on the fine sand of the crest of a ridge. Similarly, differences in lime content or in other chemical properties, either in the surface layer or lower in the profile, may strongly differentiate soils of the same class. The influence of different combinations of these disturbing factors may be observed in the wide variations in site index of the aspen on the same soil classes and in the systematic tendency for the site indices to be higher on the gray than on the red drift (fig. 8). Notwithstanding the discrepancies just mentioned, the soil classes of an upland well-drained area of uniform geological origin, that is of glacial material of the same age, may show a high degree of correlation with the plant responses to the different habitat conditions.

CORRELATION BETWEEN TEXTURE GROUPS AND SITE INDEX

The soil classes, subdivided into red and gray drift, provide 15 groups for the determination of the correlation ratio with site index. The distribution of the plots according to site index in each of these groups arranged in sequence from the coarse to the fine textures are shown in figure 8. In table 5, they have been rearranged in ascending sequence of mean site index (MI). The correlation ratio of 0.573 is distinctly significant. The influence of the two drifts of different origin almost entirely disarranges the sequence which would be expected from texture alone as given in figure 8, or in other words, the differences in the drift within the same soil class are usually greater than the differences between successive soil classes. This suggests that texture alone may not be an adequate basis for the classification of habitats in relation to growth.

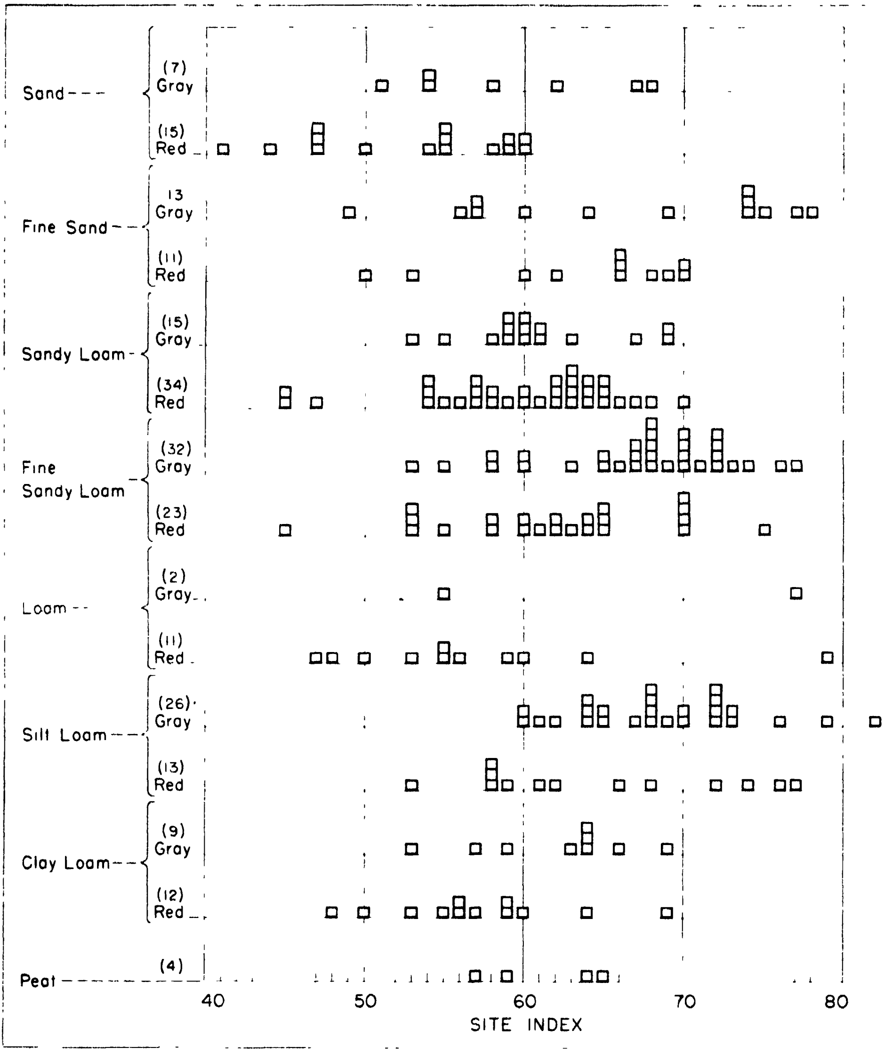

FIG. 8. Distribution of site indices by soil-texture class.

GEOLOGICAL FORMATION GROUPS

The glacial and to a minor extent other geological formations, as a basis for the classification of aspen habitats, are not wholly exclusive of texture classes. In certain groups differences in geological formation are always associated with and in fact are the cause of differences in texture classes. On the other hand, some glacial formations may be associated with several texture classes.

The nine surface formations which were distinguished were outwash, lake-bed clay, sandy moraine, rock, peat, lake-washed sandy till, lake-washed

TABLE 5. CORRELATION RATIO BETWEEN SOIL TEXTURE CLASSES AND MEAN SITE INDEX OF ASPEN

Soil class and drift	Plots (n)	Mean site index m_I	$m_I - M_I$	$(m_I - M_I)^2$	$(m_I - M_I)^2 n$
	Number				
Sand, red drift	15	52 7	—9 8	96 0	1,440 6
Loam, red drift	11	56 9	—5 6	31 4	345 0
Clay loam, red drift	12	57 2	—5 3	28 1	337 1
Sand, gray drift	7	59 1	—3 4	11 6	80 9
Sandy loam.					
Red drift	34	59 8	—2 7	7 3	247 9
Gray drift	15	60 9	—1 6	2 6	38 4
Peat	4	61 0	-1 5	2 3	9 0
Fine sandy loam, red drift	23	61 8	—0 7	0 5	11 3
Clay loam, gray drift	9	62 1	—0 4	0 2	1 4
Fine sand, red drift	11	63 6	1 1	1 2	13 3
Silt loam, red drift	13	64 8	2.3	5 3	68 8
Loam, gray drift	2	66 0	3 5	12 3	24 5
Fine sand, gray drift	13	66 5	4 0	16 0	208 0
Fine sandy loam, gray drift	32	67 1	4 6	21 2	677 1
Silt loam, gray drift	26	68 6	6 1	37 2	967 5
Σn ($-N$)	227				
M_I		62 5			
$\Sigma[(m_I - M_I)^2 n]$					4,470 8

$\sigma M_I = \sqrt{\dfrac{\Sigma[(m_I - M_I)^2 n]}{N}} = 4\ 44$ $\eta_I = \dfrac{\sigma M_I}{\sigma_I} = 0\ 573$

$\sigma_I = 7\ 75$

clayey till, clayey moraine, and till. The descriptions of these formations are familiar or are readily available in the reports of Leverett (1915) and Leverett and Sardeson (1917), for Minnesota, or in other works on glacial geology and physiography.

In their essentials for the present purpose, the outwash is a generally level deposit of deep, well-drained sand. The lake-bed clay is a deposit of clay in the beds of former lakes, level in topography and of sufficient thickness to be only slowly permeable to water and consequently having poor drainage and aeration in wet seasons. The sandy moraines are the hilly more or less assorted deposits of coarser materials, sands, and gravels, often stony. The rock formation includes the area in northeastern Minnesota where the usually igneous rocks outcrop or are within two or three feet of the surface. Peat is the postglacial accumulation of organic matter in the standing water of lakes or depressions. The lake-washed sandy till includes the sandy deposits in the shallower portions of the postglacial lakes which have been subject to wave action so that the finer materials of the original till have been removed. The lake-washed clayey till still retains much of the clayey material although it has been covered by lake waters for considerable periods. Both these deposits have level topography, and the latter in particular is apt to have deficient drainage. Clayey moraine includes the fine-textured, unassorted morainal deposits carried by and left at the retreat of the ice. Till is the unassorted

drift laid down and over-ridden by the ice, often descriptively called boulder clay.

The widely different conditions of moisture retentiveness, permeability, drainage, and aeration, and the degree to which these formations have been subjected to former water action, must evidently affect their character as plant habitats. In this respect, the first four related factors act together in differentiating the formations. Thus the formations when arranged in the following order represent increasing degrees of moisture retentiveness and decreasing degrees of permeability, drainage, and aeration: (1) Outwash, (2) sandy moraine, (3) rock, (4) till, (5) lake-washed sandy till, (6) clayey moraine, (7) lake-washed clayey till, (8) lake-bed clay, and (9) peat. Locally some differences may easily be found in the order of the middle members of the series, but in general it will hold good for these factors. The same order does not apply, however, to the amount or availability of plant nutrients, which probably reach a maximum in the till. For this and, more emphatically, for other reasons, the foregoing order does not represent an increasing or decreasing series in relation to the favorableness of the different formations as plant habitats. Evidently lack of moisture is often a limiting factor for plants on the outwash and sandy moraine and, just as truly, excessive moisture and lack of drainage become critical on the clays and on peat. The generally more favorable conditions in both respects are found near the middle of the series.

The aspen plots of each surface formation were further separated as to their location in the red or gray drift areas. The evidence of the favorable influence, presumably of the high lime content in the gray drift, will appear in figure 9, where the growth of the aspen as measured by its site index is shown for both red and gray drift of each surface formation.

CORRELATION BETWEEN GEOLOGICAL FORMATION GROUPS AND SITE INDEX

The distributions of plots according to their site indices within each formation group are shown in figure 9. In the five groups in which less than four plots occurred the red and gray drift subdivisions were combined, leaving 12 categories for the computation of correlation ratio. The essential figures are given in table 6, where they have been rearranged in ascending order of mean site index and thus do not correspond to the sequence in figure 9. In only one instance, that of the till formation, is the difference between red and gray drift greater than that between the formations themselves. Consequently, the red drift till is separated from the gray drift till by two other formations. The correlation ratio of 0.640 indicates a significant relation between the soil formations and the site indices of the aspen stands. This is a rather high degree of correlation when it is considered that soils of very different textures are grouped together in the individual formations.

If figure 9 is examined more closely, the outwash stands by itself in

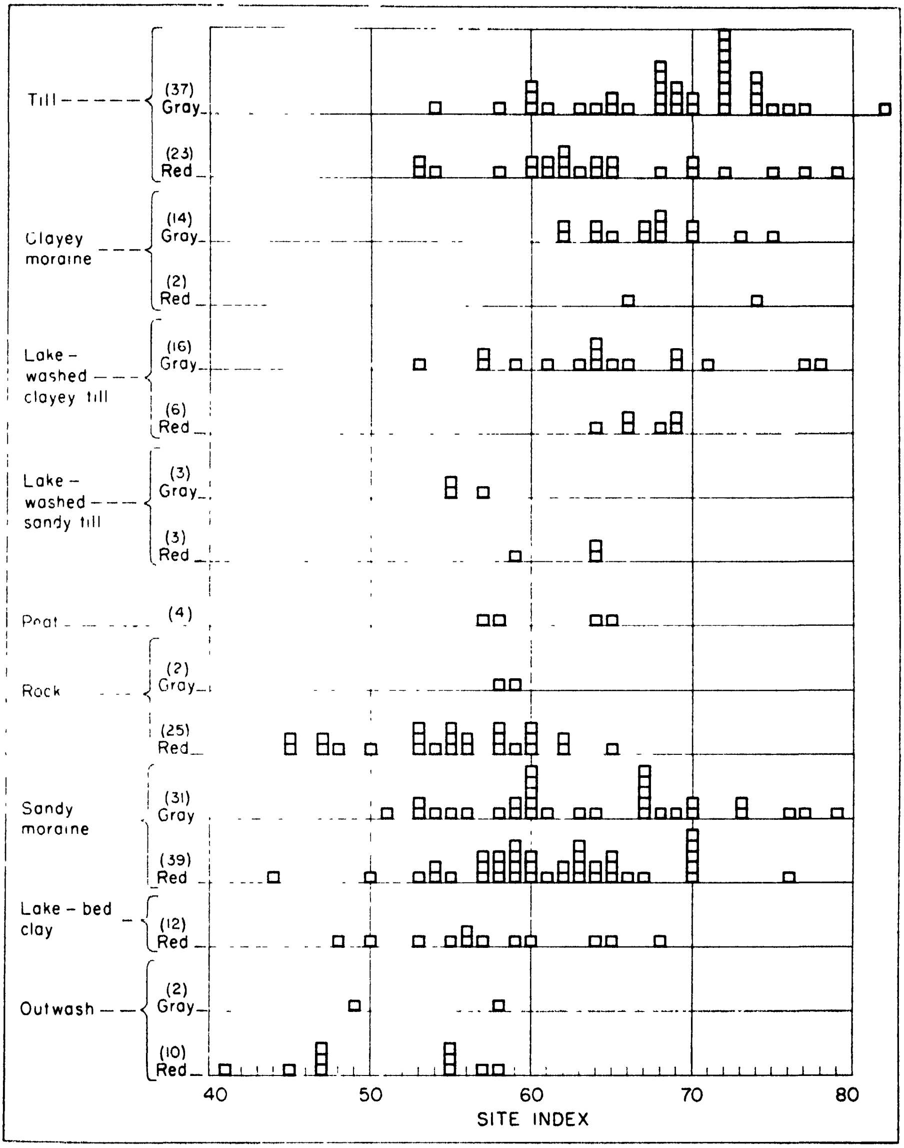

FIG. 9. Distribution of site indices by surface formation.

representing the poorest habitat for the growth of aspen. The rock and lake-bed clay are not very different and could be considered to form a group of somewhat less poor habitats. Sandy moraine, lake-washed sandy till, and peat take an intermediate place in the scale of productivity. Finally, the lake-washed clayey till, clayey moraine, and till are somewhat similar in site index and represent the favorable surface formations for the growth of aspen. It

TABLE 6. CORRELATION RATIO BETWEEN SURFACE FORMATIONS AND MEAN SITE INDEX OF ASPEN

Surface formation and drift	Plots (n)	Mean site index M_I	$m_I - M_I$	$(m_I - M_I)^2$	$(m_I - M_I)^2 n$
	Number				
Outwash, red and gray drift	12	51.2	−11.3	127.7	1,532.3
Rock, red and gray drift	27	55.2	−7.3	53.3	1,438.8
Lake-bed clay, red drift	12	57.6	−4.9	24.0	288.1
Lake-washed sandy till, red and gray drift	6	59.0	−3.5	12.3	73.5
Peat, red and gray drift	4	61.0	−1.5	2.3	9.0
Sandy moraine					
Red drift	39	61.3	−1.2	1.4	56.2
Gray drift	31	63.7	1.2	1.4	44.6
Till, red drift	23	64.3	1.8	3.2	74.5
Lake-washed clayey till					
Gray drift	16	64.8	2.3	5.3	84.6
Red drift	6	67.0	4.5	20.3	121.5
Clayey moraine, red and gray drift	16	67.7	5.2	27.0	432.6
Till, gray drift	37	68.8	6.3	39.7	1,468.5
Σn $(=N)$	229				
M_I		62.5			
$\Sigma[(m_I - M_I)^2 n]$					5,624.4

$\sigma_{M_I} = \sqrt{\dfrac{\Sigma[(m_I - M_I)^2 n]}{N}} = 4.96$ $\qquad \eta_{II} = \dfrac{\sigma_{M_I}}{\sigma_I} = 0.640$

$\sigma_I = 7.75$

may be noted that this is not the order of moisture and aeration relations previously discussed. The outwash with deficient moisture and the lake-bed clay with seasonally excessive moisture and lack of aeration stand close together as unfavorable habitats as measured by the growth of aspen. The favorable habitats are the lake-washed clayey till, clayey moraine, and till—formations with neither deficient nor excessive moisture, or at worst those of the latter class with reasonably good drainage.

As compared with the texture classes on the basis of the aspen site indices, the surface formations are the more closely correlated with site index, as indicated by the correlation ratio of 0.64 as compared with 0.57 for the texture classes. In other words, if it were necessary to choose between the surface formations and texture classes as a basis for the classification of soil productivity for tree growth, the surface formations would give the better correlation. The two forms of classification are obviously not mutually exclusive and are in many respects closely related, but, as a whole, the surface formations seem to integrate more completely the growth factors which influence aspen than do the texture classes.

COMBINED TEXTURE AND GEOLOGICAL-FORMATION GROUPS

If now the two preceding groupings are combined into a single series, it should be possible to find a classification on this basis which would be more closely correlated with aspen growth than were either of the foregoing series alone. This was done, by subdividing the surface formations into texture

classes and further modifying the groups thus formed by the fact already established that the gray drift as compared with the red drift caused as much difference in habitat factors as that between two adjacent soil classes. In order to avoid having more groups than could be satisfactorily treated biometrically with the data available, some of them were recombined, so that finally the following 12 groups were differentiated: On the outwash, the sands and fine sands formed one group and the sandy loam or heavier textured soils a second. On rock, one group comprised fine sands, sandy loams and loams, and a second, fine sandy loams and silt loams. Clay loam and clay on lake-bed clay formed a fifth group. The sandy moraine and lake-washed sandy till were combined for the coarser-textured classes into a group for the sands and a second for the red-drift fine sands and sandy loams. Gray-drift sandy loams on lake-washed sandy till were combined with fine sandy loams and heavier-textured soils on this and on the sandy-moraine formation. In other words, a sandy loam on the gray drift was considered to be more nearly equivalent to a fine sandy loam or loam on the red drift than to a soil of the same class on that drift. Peat was retained as a distinct group as was clay loam on lake-washed clayey till. Gray-drift sands and fine sands and red-drift sandy loams and fine sandy loams on till, clayey moraine, and lake-washed clayey till were all combined into one group. For the same three formations, the gray-drift sandy loams and fine sandy loams were grouped with the red-drift soils of textures finer than fine sandy loam, making the twelfth group.

In this grouping, the same growth factors are involved that have been discussed for the separate soil classes and surface formations, but the foregoing arrangement combines them in groups in which they reinforce and intensify one another instead of conflicting and nullifying, as was the case in the earlier classifications. For example, the sandy-texture class in combination with the outwash formation makes a more distinct group than could be had if several texture classes were included in the outwash group or if two or more surface formations were combined in a class of sands. This grouping of combinations of soil classes and geological formations is in effect a soil classification in broad categories based only on texture class and geological origin, but it serves to combine in rather distinct and homogeneous groups the more important edaphic factors which influence plant growth.

CORRELATION WITH SITE INDEX AND DIFFERENTIATION OF COMBINED TEXTURE AND GEOLOGICAL-FORMATION GROUPS

These 12 groups and the basis for the calculation of correlation ratio with site index are arranged in table 7 in ascending order of mean site index. The distributions of plots in each group are shown in figure 10, where the group numbers correspond to those at the extreme left in table 7. This ratio of 0.699 represents a decidedly higher degree of correlation than was obtained with either of the previous groupings. The conclusion seems justified that a

TABLE 7. CORRELATION RATIO BETWEEN COMBINED TEXTURE-SURFACE FORMATION GROUPS AND MEAN SITE INDEX OF ASPEN

Soil group	Plots (n)	Mean site index m_I	$m_I - M_I$	$(m_I - M_I)^2$	$(m_I - M_I)^2 n$
	Number				
1. Sands and fine sands on red-drift outwash	7	48.7	−13.8	190.4	1,333.1
2. Sandy loam and heavier on red-drift outwash	4	53 7	− 8 8	77 4	309 8
4. Clay loam on lake-bed clay	9	54 9	− 7.6	57.8	519 8
5. Red-drift fine sandy loam and silt loam on rock	8	55 1	− 7.4	54 8	438.1
3. Red-drift fine sand, sandy loam, and loam on rock	19	55.3	− 7 2	51.8	985 0
6. Sands on sandy moraine and on lake-washed sandy till	13	55 3	− 7 2	51.8	673.9
8. Peat	4	61.0	− 1.5	2 3	9 4
7. Red-drift fine sand and sandy loam on sandy moraine and lake-washed sandy till	23	61 4	− 1 1	1 2	27 8
9. Clay loam on lake-washed clayey till	12	62.6	0 1	0 01	0 1
11. Sandy loam on gray drift; and fine sandy loam and heavier on sandy moraine or lake-washed sandy till	39	64 6	2 1	4 4	176 4
10. Sand and fine sand on gray drift; sandy loam, and fine sandy loam on red drift, on till, clayey moraine, or lake-washed clayey till	34	64.9	2 4	5 8	195.8
12. Sandy loam and fine sandy loam on gray drift; and heavier red-drift soils on till, clayey moraine, or lake-washed till	58	68 5	6 0	36.0	2,088 0
$\Sigma n (= N)$	230				
M_I	.	62 5			
$\Sigma[(m_I - M_I)^2 n]$	.	..		..	6,757.2

$\sigma_{M_I} = \sqrt{[\Sigma(m_I - M_I)^2 n]} = 5.42$ $\qquad \eta_{II} = \dfrac{\sigma_{M_I}}{\sigma_I} = 0.699$

$\sigma_I = 7.75$

combination of soil texture classes and surface formations affords a classification of the habitats of the aspen community more closely related to their productivity as measured by site index than do either soil classes or surface formations alone.

Some interesting suggestions in regard to the influence of different edaphic factors on the growth of aspen may be derived from the order in which the groups are arranged according to their mean site indices in table 7. The fact that the outwash sands, on which the aspen community is rarely found, have the lowest productivity—even the heavier textured soils on this formation being lower on the average than those of any other group—and that they have the lowest moisture-retaining capacity and are also lowest in nutrient contents of any of the groups suggests that they are close to representing limiting edaphic conditions for the species.

Next above the outwash in the site-index scale come the clay and clay loams on lake-bed clay, a group with strikingly different properties. They are chiefly the red clays of the bed of Lake Duluth, the finest textured and

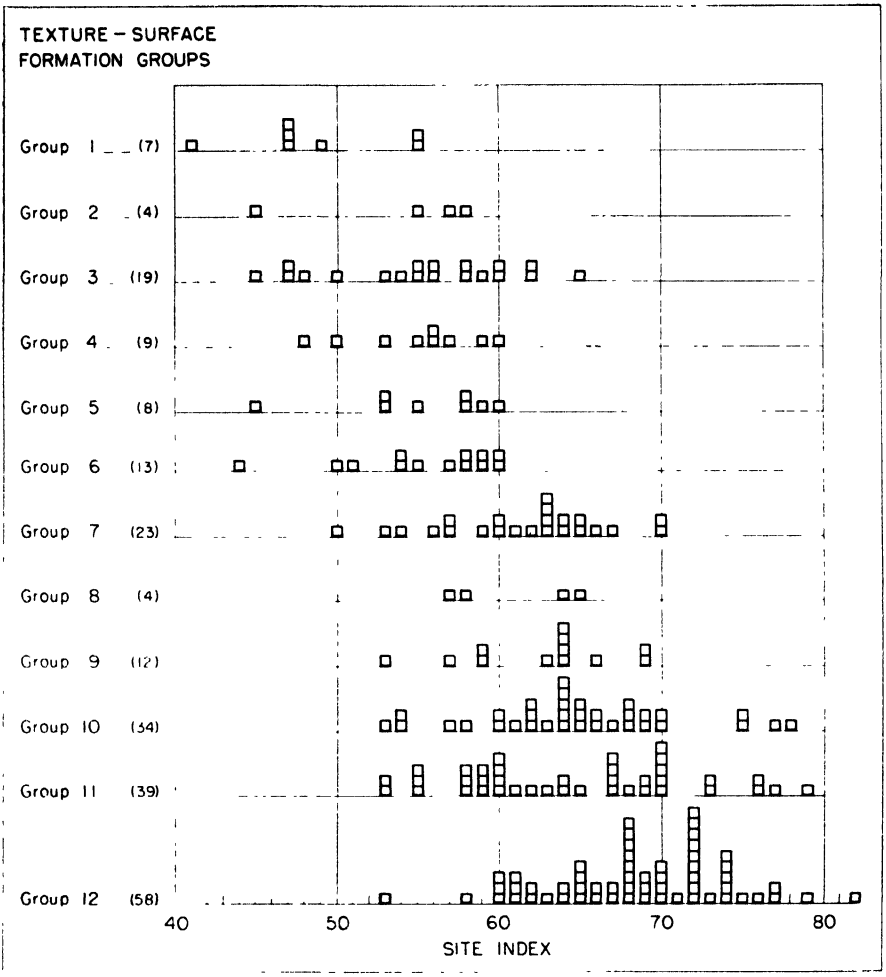

FIG. 10. Distribution of site indices by combined soil-texture and surface-formation groups.

most moisture-retentive mineral soils in the region, so much so that drainage is often poor and aeration deficient. The slow growth on this group is evidently caused by a set of factors quite different from those that were operative in the outwash groups, yet the net result as expressed in the growth of aspen is closely similar. The soils of the rock formation and the sands of the sandy moraine and lake-washed sandy till are only slightly higher than the clays. These groups, like the outwash, represent habitats not far removed from a xeric origin. Above them comes the group of fine sands and sandy loams on sandy moraine or lake-washed sandy till of the red drift, more favorable in moisture and fertility because of their finer texture. Close to this

group come the hydric peat and clay loam on lake-washed clayey till, which tend to resemble the lake-bed clay in properties and to contrast with the preceding xeric groups.

The two large mesic groups—the gray-drift sand and fine sand and red-drift sandy loam and fine sandy loam on till, clayey moraine, and lake-washed clayey till and the gray-drift sandy loam and fine sandy loam and heavier soils on sandy moraine or lake-washed sandy till—are respectively the lighter texture classes on the less permeable formations and the heavier texture classes on the more permeable formations, an example in their identity of site index, of the reciprocal effect of surface texture and underlying glacial deposit.

Finally the most favorable habitats as measured by aspen growth are included in the group of sandy loams and fine sandy loams of the gray drift and the heavier red-drift soils on till, clayey moraine, or lake-washed till. This is the group of mesic or slightly hydro-mesic formations with mesic surface-soil layers, which might be expected to favor the development of aspen or of any other mesic community.

Are these 12 groups distinct, considering the variability and overlapping of the site-index values of the individual plots? The difference between the means of any two groups may be tested biometrically by computing the standard deviation of their difference. Using this measure as modified for small numbers by Fisher (1930) in what he calls the "t" test for the significance of a difference between two means, "t" is calculated (for large numbers of observations it is simply the ratio between the difference of the two means and the standard deviation of that difference) and, from its value and that of "n," the number of degrees of freedom in the two series, the probability that the difference may be due to chance. An example will make clear the method of calculation and the interpretation. In the first two groups in figure 10, there are 7 and 4 site-index values respectively, and therefore the degrees of freedom are $n_1 = 6$ and $n_2 = 3$. The corresponding mean values of site index are $M_{I_1} = 48.7$ and $M_{I_2} = 53.7$, and $M_{I_2} - M_{I_1} = 5.0$. $n = n_1 + n_2 = 6 + 3 = 9$. Then —

$$\Sigma(I_1 - M_{I_1})^2 = \Sigma I_1^2 - (n_1 + 1)M^2_{I_1} = 16{,}759 - 7(48.7)^2 = 155$$
$$\Sigma(I_2 - M_{I_2})^2 = \Sigma I_2^2 - (n_2 + 1)M^2_{I_1} = 11{,}663 - 4(53.7)^2 = 127$$
$$\Sigma(I_1 - M_{I_1})^2 + \Sigma(I_2 - M_{I_2})^2 = \overline{282}$$

The square of the standard deviation of the difference is—

$$\sigma^2_{(M_{I_2} - M_{I_1})} \left(\frac{1}{n_1 + 1} + \frac{1}{n_2 + 1}\right) = \frac{n_1 + n_2 + 2}{(n_1 + 1)(n_2 + 1)(n_1 + n_2)}$$

$$\left[\Sigma(I_1 - M_{I_1})^2 + \Sigma(I_2 - M_{I_2})^2\right] = 12.3, \text{ and t} =$$

$$\frac{M_{I_2} - M_{I_1}}{\sigma(M_{I_2} - M_{I_1})\sqrt{\frac{1}{n_1+1} + \frac{1}{n_2+1}}} = \frac{5.0}{\sqrt{12.3}} = 1.43.$$

Then from Fisher's table IV for this value of "t" and $n = 9$, we find $P = 0.2$, which is to say that the chances are 20 in 100 that the difference between the mean site indices of the first two soil groups may be due wholly to random errors of sampling. If a probability of 0.05 or 5 chances in 100 is accepted as the limit for deciding whether or not a difference is significant, then clearly the sands and fine sands are not significantly different from the sandy loams and heavier soils on the outwash formation. This criterion of differences is, of course, based entirely upon the variability of the site index value of the two soil groups being tested, and shows nothing except in that way as to the logic or lack of logic in the physical or biological relationships between them. Actually, in this instance the surface formation is the same in both groups while the texture classes are different, so that they have a bond of relationship and the difference between them might logically be expected to be small.

Similar tests were made as to the significance of the differences between each two groups where there seemed to be any question. A summary of the results is given below in table 8, using the numbers as given in figure 10 and table 7 to designate the different soil groups.

TABLE 8. SUMMARY OF TEST OF DIFFERENCE IN SOIL GROUPS

Soil groups	$M_{I_2} - M_{I_1}$	n_2	n_1	n	t	P	Significance of difference
2 – 1	5.0	3	6	9	1.43	0.2	—
3 – 2	1.6	18	3	21	0.53	0.6	—
4 – 1	6.2	8	6	14	2.81	0.02	+
8 – 6	5.7	3	12	15	2.12	0.05	+
10 – 8	3.9	33	3	36	1.21	0.24	—
12 – 10	3.6	57	33	90	2.43	0.02	+
I – II	4.8	57	111	168	5.0	0.01—	+
II – III	8.6	111	52	163	9.8	0.01—	+
III – IV	3.4	52	6	58	6.4	0.01—	+

From the upper section of the table it may be concluded, first, that group 2 is not significantly different from group 1, and second, that group 3 is not significantly different from 2. Group 4, however, is significantly different from group 1, and as groups 3, 5, and 6 are higher in mean site index than 3, they also may be assumed to be significantly different from 1. Group 8, the lowest of the remaining groups, is significantly different from group 6, the highest of the preceding groups. Between 6 and 8 then, is a line of division not only between those two groups but between the several which are adjacent to them or, if it were desirable, between two parts into which the whole array of plots could be divided. Finally group 12 is significantly different from 10 and also from 11 and 9, 8 and 7. On the basis of these tests, then, larger

groupings were made, each containing one or more of the original groups. Each of these groupings when tested by the same "t" test in the lower portion of the foregoing tabulation proves to be significantly different from the others.

From the practical standpoint in the determination of forest productivity or site quality for the growth of aspen, it would be highly desirable and convenient to be able to classify the aspen lands in four distinct site qualities on the basis of soil texture and surface formation. It will be interesting to see, however, if these groupings have any physical and biological homogeneity or if they must be considered as artificial categories without such unity. For the moment these combined groups may be called site qualities. Then site quality I includes only group 12, consisting of sandy loams and fine sandy loams of the gray drift and the heavier red-drift soils on till, clayey moraine, or on lake-washed till, and can be considered a homogeneous natural unit. Site quality II includes groups 7, 8, 9, 10, and 11. Among these appear such diverse groups as peat and clay loam on lake-washed clayey till on the hydric side and fine sand and sandy loam on sandy moraine on the xeric side. This site quality obviously cannot be considered to be made up of a grouping of unified natural habitats. It happens to be quite uniform in respect to the growth of aspen but this uniformity is the resultant of the combined effects of very different combinations of factors. Site quality III includes groups 3, 4, 5, and 6 and because 2 has been shown to be much nearer 3 than 1, it is also included.

Here again the component groups make a heterogeneous combination. On the xeric side are the sandy loams on outwash and the sands on sandy moraine, and on the hydric, the clay loams and clays on lake-bed clay. Furthermore, the two groups on the rock formation are also included which are quite different from either of the foregoing groups. As in site quality II, this grouping also has no natural homogeneity except as to the growth of aspen. Site quality I comprises only the one group of sands and fine sands on outwash and is therefore a natural unit. It would, of course, be possible to separate site qualities II and III into their xeric and hydric components and thereby establish a somewhat larger number of categories (but still less than 12). These would have some biological homogeneity but would only in part be distinguishable by the site index of the aspen. Thus far the conclusion is suggested that the growth rate of aspen will serve to differentiate the habitats into four rather broad categories which cannot be considered to have natural homogeneity.

The relationship between the 12 groups based on soil texture and geological formation may also be tested by another biometrical device. Pearson (1906-7) has suggested a method of determining the significance of the difference between a subsample and the whole sample of which it forms a part. By this method the significance of the difference between the mean site

index for each group and that of the whole sample of 230 plots was computed. Algebraically the function may be represented by the expression—

$$\frac{m_I - M_I}{\sqrt{\frac{\sigma_n^2}{n} - \frac{2\sigma_n^2 - \sigma_N^2}{N} - \frac{n(M_I - m_I)^2}{N(N-n)}}}$$

This is in effect the ratio of the actual difference between the means of subsample and sample divided by the standard deviation of the difference of those means corrected for the influence of the relationship between sample and subsample. The foregoing formula makes no allowance for small numbers of cases, hence the values for those groups with only a few plots may not be wholly reliable. The essentials of the computation and the results are shown in table 9. The statistical constants for the whole 230 plots, are $N = 230$,

TABLE 9. THE SIGNIFICANCE OF THE DIFFERENCE BETWEEN THE MEAN SITE INDEX OF EACH GROUP AS A SUBSAMPLE AND ALL OF THE PLOTS AS A SAMPLE

Soil group	$m_I - M_I$	n	$\frac{\sigma_n^2}{n}$	$\frac{2\sigma_n^2 - \sigma_N^2}{N}$	$\frac{n(M_I - m_I)^2}{N(N-n)}$	c	$\frac{m_I - M_I}{\sqrt{c}}$
1	−13.8	7	3.20	+0.07	−0.03	3.24	−7.6
2	− 8.8	4	8.02	− .02	− .01	7.99	−3.1
3	− 7.2	19	1.4	+ .03	− .02	1.5	−6.0
4	− 7.6	9	1.4	+ .15	− .01	1.54	−6.1
5	− 7.4	8	3.0	+ .06	− .01	3.05	−4.2
6	− 7.2	13	1.6	+ .08	− .01	1.67	−5.6
7	− 1.1	23	1.1	+ .05	.00	1.15	−1.0
8	− 1.5	4	3.1	+ .15	.00	3.25	−0.8
9	+ 0.1	12	1.5	+ .10	.00	1.60	+0.1
10	+ 2.4	34	1.1	− .07	.00	1.03	+1.9
11	+ 2.1	39	1.2	− .14	.00	1.06	+2.0
12	+ 6.0	58	0.6	− .03	− .05	0.52	+8.3

$M_I = 62.5$ and $\sigma_N^2 = 60.06$. For convenience the long expression under the radical in the denominator of the formula will be designated by "c". "m_I" is the mean site index for a group, and "n" is the number of plots in a group. The standard deviation of a group is designated σ_n.

The fact that the values of the ratio in the last column form a progressive series, increasing from −7.6 to 0 and on up to +8.3, is in itself a demonstration that the groups have a systematic arrangement and progression of the mean site-index values. The two erratic values for groups 2 and 5 are doubtless caused by the small number of cases and consequently abnormal distributions from which the biometric constants had to be calculated. The same four groupings or site qualities which were indicated by the significant differences between groups may also be distinguished by this method. Group 1 with a ratio of − 7.6 stands by itself. Groups 2, 3, 4, 5, and 6 with ratios from − 6.1 to − 3.1 (probably low) may logically be combined. Groups 7, 8, 9, 10, and 11 with values from − 1.0 to 2.0 form a third grouping, and group

12 with a ratio of 8.3 makes the fourth. The two methods therefore confirm one another, in showing that the site-index values of aspen serve to differentiate broad groupings of habitats, but, as previously pointed out, these groupings are not physically and biologically homogeneous.

CORRELATION BETWEEN COMBINED TEXTURE AND GEOLOGICAL FORMATION GROUPS AND VOLUME INDEX

For the same 12 habitat groups, the mean-volume indices were determined from the distributions of the individual plot-volume indices of the 151 well-stocked plots. The distributions are shown in figure 11. The wide dispersion

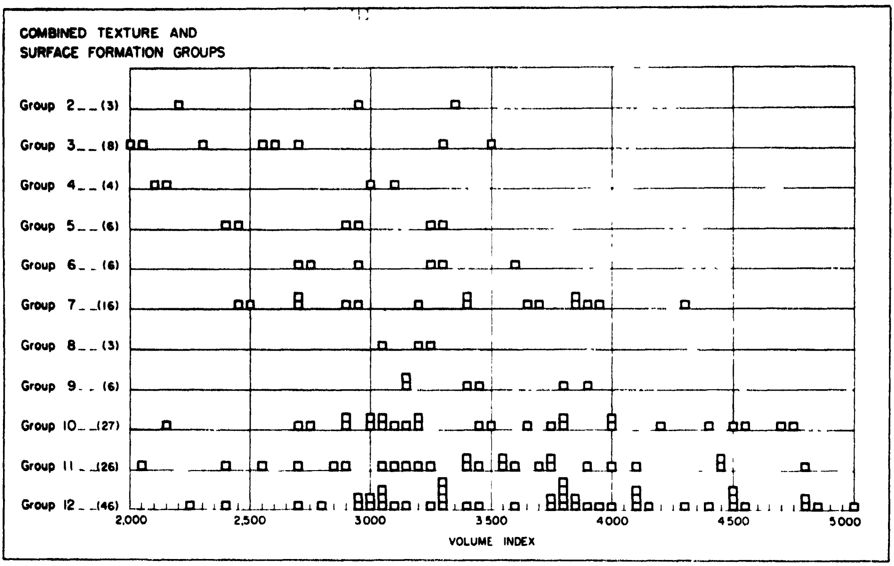

FIG. 11. Distribution of volume indices by combined soil-texture and surface-formation groups.

of volume indices in almost all of the soil groups is noticeable. Group 1 did not have any well-stocked plots and therefore is not represented. The essential figures for the computation of the correlation ratio between mean volume index and the texture-surface formation groups are shown in table 10. The soil groups are arranged in ascending order of mean volume index. The numbers in parentheses are those of the soil groups as they have been used in the foregoing discussions. Some changes in order have been made as a result of using volume index instead of site index, but the changes are in those groups which are closely adjacent and in which no significant difference between the means could be shown.

The correlation ratio between the soil texture-surface formation groups and volume index of 0.46 may be compared with the corresponding figure of 0.70 obtained in the correlation of the same soil groups with site index. The

TABLE 10. CORRELATION RATIO BETWEEN SURFACE FORMATION-TEXTURE GROUPS AND VOLUME INDEX

Soil group	Plots (n)	Mean volume index m_I	$m_I - M_I$	$(m_I - M_I)^2$	$(m_I - M_I)^2 n$
	Number				
Sands and fine sands on red drift outwash (1)	0	..	.		.
Clay loam on lake-bed clay (4)	4	2,593	801	641,601	2,566,404
Red drift fine sand, sandy loam and loam on rock (3)	8	2,619	775	600,625	4,805,000
Sandy loam and heavier on red drift outwash (2)	3	2,837	557	310,249	930,747
Red drift fine sandy loam and silt loam on rock (5)	6	2,870	524	274,576	1,227,456
Sands on sandy moraine and on lake-washed sandy till (6)	6	3,090	304	92,416	554,496
Peat (8)	3	3,160	234	54,756	164,268
Red drift fine sand and sandy loam on sandy moraine and on lake-washed sandy till (7)	16	3,335	59	3,481	55,696
Sandy loam on gray drift and fine sandy loam and heavier on sandy moraine or on lake-washed sandy till (11)	26	3,426	32	1,024	16,384
Clay loam on lake-washed clayey till (9)	6	3,467	73	5,329	31,974
Sand and fine sand on gray drift, sandy loam and fine sandy loam on red drift, on till, clayey moraine or lake-washed clayey till (10)	27	3,529	135	18,225	492,075
Sandy loam and fine sandy loam on gray drift and heavier red drift soils on till, clayey moraine or on lake-washed till (12)	46	3,670	276	76,176	3,504,096
$\Sigma n (= N)$	151				
M_I		3,394			
$\Sigma[(m_I - M_I)^2 n]$					14,348,596

$\sigma_{M_I} = \sqrt{\frac{\Sigma(m_I - M_I)^2 n}{N}} = 308.3$ $\eta_{It} = \frac{\sigma_{M_I}}{\sigma_I} = 0.461$

$\sigma_I = 669.4$

considerable difference is probably caused in large part by the wider dispersion of the individual volume-index values within groups and in the whole array than of the site-index values. This was anticipated in a previous section where the coefficients of variation were found to be 19.8 percent for the volume-index series and 12.4 percent for the site-index series. Moreover, the advantage in favor of the site index holds notwithstanding the fact that the volume-index data are limited to the well-stocked plots, a more homogeneous group, at least with respect to variations in density. The conclusion seems to be substantiated that site index is a more reliable and more distinctive criterion of aspen growth as a measure of the productivity of habitats than is stem volume growth.

SOIL PROFILE GROUPS

The soil profile, as an integrated expression of all the factors of the local environment which have had time to express themselves, should theoretically give a closer correlation with plant growth than the previously discussed soil groups which have been based on only a part of the habitat factors. The soil

types described in the more recent soil surveys have uniform profiles within rather narrow limits of variation.

SOIL TYPES AS PROFILE UNITS

At least the variation in the profile within any soil type is less than the differences which exist between soil types. The soil type will therefore be considered to represent a profile unit and the smallest habitat unit which will be considered. Any difference in the texture, geological formation, ground water, or chemical and biological activity, including the influence of the higher vegetation, will be reflected in the profiles and in a differentiation of soil types if the soil-forming processes have been sufficiently prolonged or intense.

The 277 plots of the aspen community represent 54 different soil types, and probably the number would be a little larger if detailed soil surveys had been available for all the areas from which the samples were taken. This seems like a large number of habitats on which to find a community dominated by the same species, but it is quite certain that if the study had been extended to eastern Wisconsin and adjacent Michigan the number would have been more than doubled. In the absence of soil surveys, local geographic names were given to soil types which were evidently distinct from any that had been described. The list of types and the distribution of site indices of the aspen plots on each of them, arranged in 22 groups in ascending order of median site index, are shown in figure 12.

Again the variation of site index within the same soil type and the overlapping of the distributions of adjacent types is evident, as it has been in each of the foregoing coarser classifications. The finer subdivisions of the material into something approaching the smallest units of habitat which could be conveniently distinguished as representing a community does not eliminate the variability which results in part from variations within a single soil type and in part from biological variations in the aspen species and individuals. This degree of refinement in classification has already caused the distribution of the plots in so many classes that biometrical measures would be almost meaningless for most of the classes. Further subdivision would only increase the difficulty. The suggestion of most interest to be derived from these considerations is that no single or average measure of the growth of trees or vegetation is specifically applicable to any other habitat than the particular one in which the trees are growing and no attainable refinement of classification is likely to make it applicable. With the amount of material available, therefore, it becomes necessary to devise a classification of soil profiles into less numerous categories than are afforded by the soil types.

SCHEME OF GROUPING BASED ON PROFILE FEATURES

The soil profile descriptions offer a wealth of material upon which to base a classification. Each of the four or more horizons is characterized as to

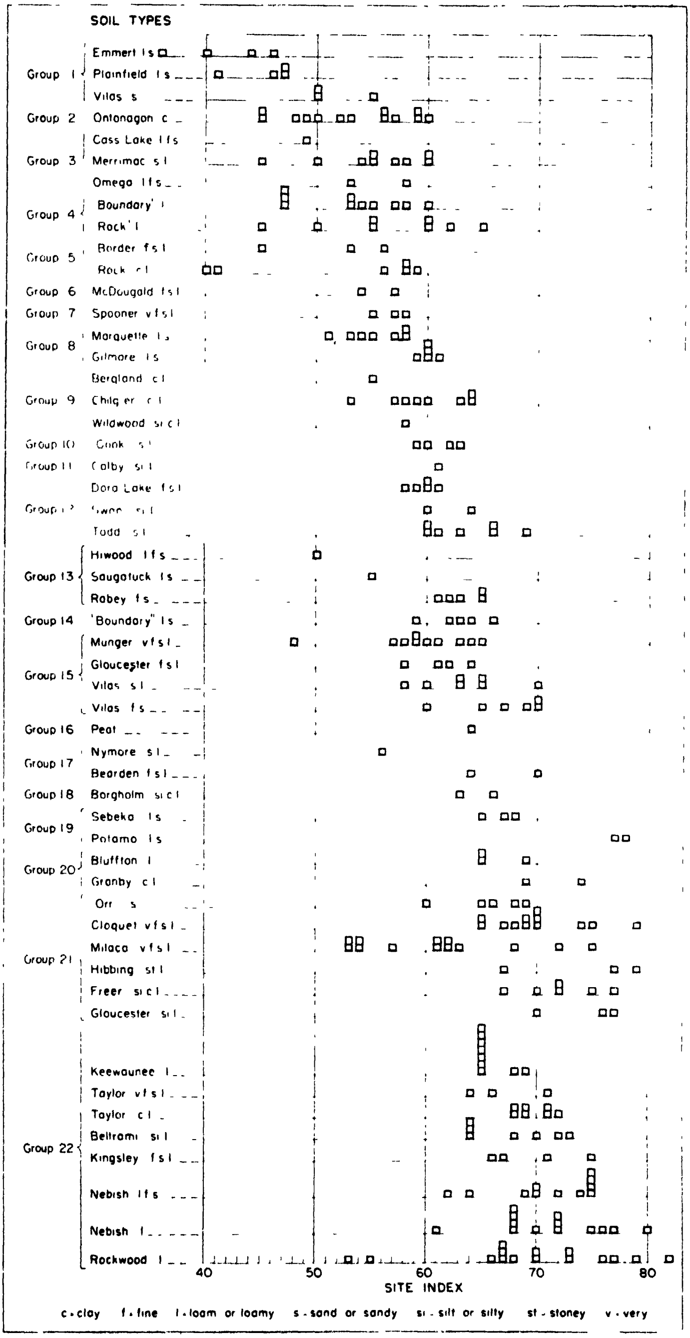

FIG. 12. Distribution of 277 aspen plots, by site index, in 54 different soil types, classified in 22 groups.

thickness, texture, color, consistency, and certain easily determined chemical and biological particulars. Fortunately certain combinations of these features are associated; in those cases it is only necessary to decide which are most significant and convenient. The different horizons of the profiles will be designated by the Russian system of letters and subscripts, which is probably in more general use in the United States than any other one system.

The A_0 horizon of organic matter at the surface has few distinguishing characteristics within a relatively uniform community like the aspen, except in situations of excessive moisture where it becomes abnormally thick with the formation of peat. The A_1 horizon includes the upper layer of mineral soil, which is dark-colored owing to its high content of organic matter. This layer is ordinarily thin in the podsolic soils but becomes distinctively thick in some of the swamp-margin soils. The A_2 horizon of eluviation varies markedly with changes in environmental influences and hence is useful for classification. Strong development of the A_2 is indicated by the light gray color and the degree of contrast and sharpness of the transition to the underlying horizon. Poor development, on the contrary, lacks these distinctive features. The horizon is thin and often grades imperceptibly into the underlying B horizon. In this region the soils with poorly developed A_2 horizon are associated with certain of the xeric and hydric habitats, whereas those with a strong A_2 are in the mesic group.

The intensity of development of the B horizon of illuviation is closely related to the A_2 horizon, that is, strong development of the A_2 is associated with strong development of the B, with certain exceptions to be noted. For the present purpose the characteristics of the B horizon seem to offer little that is not as well distinguished by the A_2 horizon, and therefore the B does not appear in the following categories of classification. The notable exception of which use has been made is the occurrence of a G or glei horizon in place of the B horizon in those soils which have developed under the influence of a high water table. The glei horizon is characteristically grayish or greenish with streaks and mottlings of yellow, orange, and rust brown. The C horizon of unweathered parent material underlying the solum is important chiefly in respect to its texture, water-holding capacity, and lime content. These features are made the basis for division of the C horizon into sandy, clayey, and rock. Subdivisions of each are designated as calcareous and noncalcareous. The soils with clayey calcareous C horizon were further separated into two classes—well-drained and poorly drained. In certain groups the sands are separated from the heavier soils.

The resulting classification of soil profiles and the soil types which belong in each of the 22 categories are shown in table 11. This serves not only to group the soil types but also to characterize them as to their profile characteristics and indicate those which are related. The degree of relationship is

TABLE 11. CLASSIFICATION OF SOIL PROFILES[1]

Character of C horizon	XERIC Weak A_2 horizon		MESIC Strong A_2 horizon		HYDRIC Weak A_2 horizon	
	Sands	Heavier soils	Without glei horizon	With glei horizon	A_0 thin, A_1 thick	A_0 thick, A_1 thin
Sandy Noncalcareous	GROUP 1— Emmert l.s. Plainfield l.t.s Vilas s.	GROUP 3— Merrimac s.l. Omega l.f s Cass Lake l f s	GROUP 15— Gloucester f.s.l. Vilas sandy l.&f.s Munger v f. s l.	GROUP 13— Saugatuck l.s. Hiwood l.f.s. Rabey f s		GROUP 16— Peat
Calcareous	GROUP 18— Marquette l.s. Gilmore l.s.	GROUP 17— Nymore s.l. Bearden f.s.l.	GROUP 12— Dora Lake f.s l. Swan si.l. Todd s.l.	GROUP 19— Sebeka l s. Potamo l.s.	GROUP 20— Bluffton l. Granby c.l.	
Rock Noncalcareous	GROUP 14— "Boundary" l s.	GROUP 4— "Rock" l. "Boundary" l.	GROUP 5— "Rock" c.l. "Border" f s l			
Clayey Noncalcareous		GROUP 10— "Cook" s.l.	GROUP 21— "Orr" s. Cloquet v.f.s.l Milaca v f.s.l. Hibbing st l. Gloucester si.l. Freer si. c.l.	GROUP 11— Colby si l	GROUP 18— Borgholm si c l	
Calcareous Well-drained			GROUP 22— Rockwood l. Nebis loam & l.f.s. Beltrami silt l Taylor cl l & v.f.s l Kingsley f s.l. Keewaunee l			
Poorly drained		GROUP 2— Ontonagon c.	GROUP 6— McDougald f s l.	GROUP 7— Spooner v f.s.l	GROUP 19— Bergland c.l. Chilgren c.l. Wildwood si c l	

[1] In this table, c. = clay, f. = fine, l = loam or loamy, s = sand or sandy; si. = silt or silty, st. = stony, v. = very

here based on soil profile features; whether it also corresponds to differences in aspen growth and plant indicators will appear later.

In the arrangement of the cross-classification in table 11, the attempt is made to follow a systematic progression of certain important factors of the habitat. Thus, in progressing from left to right, whether in the main headings or in their subdivisions, there is always an increase in soil moisture in one form or another, and under each main heading the heavier-textured types are to the right of the less moisture-retentive. The glei soil types with high water table are placed to the right of those without glei horizons and with deep ground water. The peat with excessive moisture appears at the extreme right, preceded to the left by those soil types which also have excessive moisture but not in sufficient amount for the formation of thick peat.

Similarly, in passing from higher to lower categories, in column 1 (character of C horizon) there is a progressive decrease in permeability associated

chiefly with texture and to a less degree with lime content. The relative position of rock and clay groups may be questioned, and in this case there is more variation within the groups than between them. On the whole, however, it seems that the rock areas are somewhat better drained than most of the types with clayey substrata.

The blanks in this classification are partly and perhaps wholly due to the limited variety of habitats sampled. Certainly a slight extension of the region sampled would have disclosed soils of the Miami series in eastern Wisconsin which would fall in the space for xeric, weak A_2 with clayey, calcareous C horizon; and of the Longrie series, in the space for xeric with weak A_2 and calcareous rock C horizon.

The significance of these groups in relation to habitat and growth factors has already been discussed in part in the preceding paragraph and in earlier pages in connection with the influence of texture and geological formation on habitat factors. Soil moisture in this grouping is still one of the most important factors, being controlled to a large degree by the texture of the different layers of the profile, including the C horizon.

The distinction between calcareous and noncalcareous subsoils is somewhat complex in relation to the growth factors. For one thing, a higher content of lime in any part of the profile improves the physical condition of soil, contributing to favorable granular structure in fine-textured soils and increasing the retentive capacity of sandy soils. It tends to render certain mineral nutrients more available. It reduces the hydrogen ion concentration. It stimulates the oxidation processes, and thereby the decomposition of organic matter, both carbohydrate and nitrogenous materials. Nitrogen fixation by the nodule bacteria of the Leguminosae increases with increase in lime content of the soil, and active basic material is essential for the biological transformation of ammonia to nitrate nitrogen. In a region of humid climate such as the one under consideration, the influence of lime in the soil is the resultant of several or all of these effects in combination. Ample evidence is available of the beneficial effects of lime on plant growth in acid soils. The work of Valmari (1921) in Finland, mentioned in an earlier section, demonstrated it for the yield of forests of pine and birch. The higher site indices in the same texture class on the high-lime gray drift as compared with the low-lime red drift are probably the result of greater lime content in the soil. The lime content of the C horizon is used and is believed to be the most useful criterion of the influence of lime because in almost all of the soils sampled the weathering process has removed most of the lime from the A and upper part of the B horizon to a depth varying from 2 to 5 feet. In the soils with calcareous C horizon, a relatively ample supply of lime is within reach of the deeper roots. Indirectly, this supply tends to counterbalance a possible deficiency in the upper horizons because the lime is taken up by the deeper roots, transported to the leaves, returned to the surface layers of the soil when the leaves fall and decompose, and again carried downward in the leaching process.

The glei horizon, when present, is evidence of intermittent and prolonged saturation of the soil from that depth downward by ground water. Ordinarily this horizon is found at depths of 1 to 3 feet. In the heavier-textured, moisture-retentive soils it tends to be an unfavorable factor of the habitat, doubtless because it contributes to deficient aeration. In sandy soils, on the contrary, an ample moisture supply within reach of the roots is almost always beneficial in obviating damage or mortality in critical periods of drought and in stimulating growth at other times.

Finally, the degree of development or podsolization of the A_2 horizon requires some discussion in its relation to habitat and growth factors. In the Russian work on the degradation of tchernozem, reviewed by Glinka (1927), the development of the podsolic profile under the influence of forest cover in place of the black soils of the steppes has been considered unfavorable to the growth factors. In Scandinavia and western European countries, the podsol profile under a layer of raw-humus has been associated with poorer growing conditions and lower forest yields than has the brown-earth profile with a mull layer and higher nutrient contents in the upper horizons. These conditions, however, do not correspond to those in the region under consideration. For one thing there is no raw-humus on the soils of the aspen community and, in its absence, it is by no means certain that the podsolization process is now going on in these soils. On the contrary, it seems likely that the reverse process may be in progress by which the podsolic profiles formed under an earlier and different climate and vegetation are now being transformed into mull, brown-earth profiles under the influence of a relatively mild, dry climate and of deciduous forest vegetation. If this is the case and the podsolic profiles are only relics, little importance can be ascribed to them as indicating growing conditions of the habitats.

Actually it appears that the well-developed podsolic profiles of the areas sampled include the more rather than the less favorable habitats in comparison with the profiles having weakly developed A_2 horizon. The result of this comparison, however, seems to be caused not so much by the intensity of the podsolization and degradation process in the podsolic soils as by the past and present conditions in the weakly podsolized profiles which have been unfavorable to the podsolization process. In this latter group on the xeric side are the excessively drained sands where the percolation of water is so free and rapid that podsolization is slow and ineffective. On the hydric side are the soils with high water table in which excessive moisture has prevented podsolization. In both cases the same factors which have affected the soil development have acted directly rather than indirectly through the soil-forming processes to render the habitats unfavorable for plant growth. Thus the soils with podsolized profiles remain as a group of less unfavorable rather than of more favorable soils, and there is no conflict with the well-supported and generally accepted theory that podsolization is a process of degradation.

The 22 soil-profile groups thus formed, although they are not edaphic units of the same degree as the soil types, still have homogeneity in respect to the several important soil characteristics upon which the classification is based. Moreover, the number of groups is reduced to such a point that sufficient plots are available in most of them to permit biometric analysis.

CORRELATION WITH SITE INDEX AND DIFFERENTIATION OF SOIL-PROFILE GROUPS

The distribution of the site-index values for each of the soil-profile groups, with indices of little significance omitted, is shown in figure 13. In table 12

TABLE 12. CORRELATION RATIO BETWEEN 22 SOIL-PROFILE GROUPS AND SITE INDEX

Soil-profile group	Plots (n)	Mean site index (m_I)	m_I-M_I	$(m_I$-$M_I)^2$	$(m_I$-$M_I)^2 n$
	Number				
1. A_2 weak, C sandy, acid, sands and fine sands, xeric	8	47.6	—14.9	222.0	1,776.0
4. A_2 weak, C rock, acid, loams, xeric	18	54.7	— 7.8	60.8	1,094.4
3. A_2 weak, C sandy, acid, loamy fine sands or sandy loams, xeric	11	54.9	— 7.6	57.8	635.8
5. A_2 strong, C rock, acid, no glei, mesic	7	55.0	— 7.5	56.3	394.1
2. A_2 weak, C clayey, calcareous, clays	9	55.3	— 7.2	51.8	466.2
6. A_2 strong, C clayey, calcareous, no glei, drainage poor	2	55.5	— 7.0	49.0	98.0
7. A_2 strong, C clayey, calcareous, glei	3	56.7	— 5.8	33.6	100.8
8. A_2 weak, xeric, C sandy, calcareous, sands	10	56.8	— 5.7	32.5	325.0
9. A_2 weak, hydric, C clayey, calcareous	9	59.2	— 3.3	10.9	98.1
10. A_2 weak, xeric, C clayey, acid, sandy loam	4	61.0	— 1.5	2.3	9.2
11. A_2 strong, C. clayey, acid, glei.	1	61.0	— 1.5	2.3	2.3
15. A_2 strong, C sandy, acid, no glei.	19	61.8	— .7	.5	9.3
13. A_2 strong, C sandy, acid, glei	5	62.0	— .5	.3	1.3
12. A_2 strong, C sandy, calcareous, no glei	14	62.1	— .4	.2	2.2
14. A_2 weak, xeric, C rock, acid, sands	5	62.8	.3	.1	.5
17. A_2 weak, xeric, C sandy, calcareous, sandy and fine sandy loams	3	63.3	.8	.6	1.9
16. A_2 weak, hydric, A_0 thick	1	64.0	1.5	2.3	2.3
18. A_2 weak, hydric, A_0 thin, C clayey, acid	1	66.0	3.5	12.3	12.3
21. A_2 strong, C clayey, acid, no glei, sandy loams and heavier	24	66.7	4.2	17.6	422.4
20. A_2 weak, hydric, A_0 thin, C sandy, calcareous	5	68.4	5.9	34.8	174.0
22. A_2 strong, C clayey, calcareous, sandy loams, and heavier, no glei	66	68.9	6.4	41.0	2,706.0
19. A_2 strong, C sandy, calcareous, glei	5	71.0	8.5	72.3	361.5
$\Sigma n(=N)$	230	....	.....	..	...
$\Sigma[(m_I$-$M_I)^2 n]$	..	...	......	..	8,693.6

$$\sigma_{M_I} = \sqrt{\frac{\Sigma[(m_I - M_I)^2 n]}{N}} = 6.15 \qquad \eta = \frac{\sigma_{M_I}}{\sigma_I} = 0.795$$

$$\sigma_I = \sqrt{\frac{\Sigma I^2}{N} - M^2_I} = 7.74$$

$$M_I = 62.5$$

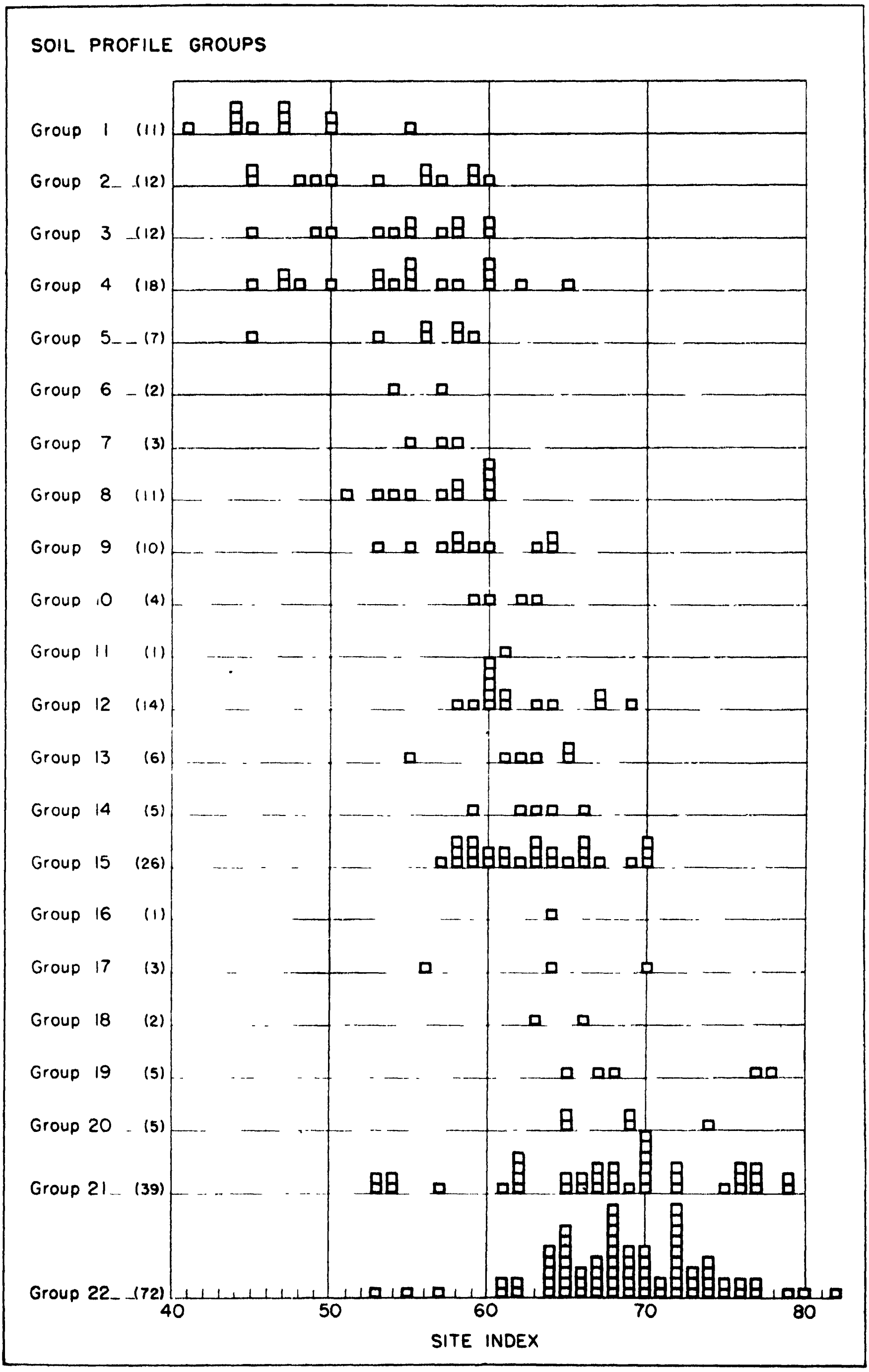

FIG. 13. Distribution of site indices by soil-profile groups.

these are arranged in ascending order of mean site index. The three site-index groups having the lowest mean site indices in the series are all xeric, with weak development of the A_2 horizon, and acid (used in the sense of noncalcareous for the sake of brevity). The fourth soil-profile group is also acid and the rock substratum at shallow depths seems to offset the less unfavorable characteristics indicated by moderate moisture conditions and strong development of the A_2 horizon. The fifth has a weak A_2 and, although calcareous, is rendered unfavorable by the impervious and poorly aerated clay texture on a clayey parent material. Starting at the upper end of the series, the two highest groups are both calcareous with strong A_2 horizons, one with a sandy substratum and high water table, the other with clayey substratum and favorable texture (sandy loam or heavier) in the upper layers. The third is also calcareous but is a hydric group with weak A_2 on a sandy parent material. The fourth is acid with strong A_2 and good texture conditions on a clayey substratum. Various combinations of characteristics typify the intermediate groups.

It is evident from what has been said and from an examination of table 12 that no one profile feature by itself has sufficient weight to enable a prediction of habitat productivity. Furthermore, different combinations of features, more or less favorable in their significance ad acting with different intensities, give rise to a series of groups whose relative position in the scale of productivity could not easily be forecast. Certain indications as to the significance of the different profile features in relation to the growth factors of the habitat may, however, be derived from the mean site-index scale. Xeric conditions tend to be unfavorable for the growth of aspen, especially if they are intensified by sandy surface and subsoil and associated with a poor development of the A_2 horizon. Mesic conditions tend to be favorable. Hydric conditions tend to be favorable except where they are accompanied by deficient drainage. A strong development of the A_2 horizon is more likely to be associated with good growth, and a weak A_2 with poor growth. A calcareous subsoil tends to be more favorable than a noncalcareous. A sandy C horizon is unfavorable in association with sandy surface layers in xeric habitats but generally favorable in hydric habitats. A clayey subsoil tends to be favorable for the growth of aspen except when associated with deficient drainage. A rock substratum at shallow depths is generally unfavorable. Surface texture classes of sands, clays, and peat tend to be less favorable than the intermediate classes with certain exceptions caused by counteracting conditions of subsoil texture or moisture.

The correlation ratio between the 22 profile groups and mean site index and the essential figures for its computation are shown in table 12. The number of plots used for the calculation was limited to the same 230 which were used in the combined texture-surface formation groups so that the correlation ratios might be comparable.

This correlation ratio of 0.795 indicates a high degree of relationship between site-index and soil-profile groups. It is decidedly higher than the best correlation previously established—that of 0.699 with the combined texture and geological formation groups. In other words, profile groups in terms of the features which have been used in the classification afford a better basis for the prediction of site index or productivity of habitat than any of the other groups which have been tried.

The next step is to see how many and which of these groups are distinct from one another, as judged by the significance of the differences between their means. The process and method are the same that were used for the texture-surface formation groups. The numbers from figure 13 and table 12 are used to designate the profile groups. The essential figures are tabulated in table 13. The differences that are discussed in the following paragraph may be visualized by referring to figure 13.

TABLE 13. SIGNIFICANCES OF DIFFERENCES BETWEEN MEAN SITE INDEX VALUES OF SOIL-PROFILE GROUPS

Profile groups	$MI_2 - MI_1$	n_2	n_1	n	t	P	Significance of difference
2 - 1	7 7	8	7	15	3 5	0 01	+
4 - 1	7 1	17	7	24	3 3	01	+
8 - 4	2 1	9	17	26	1 12	28	—
9 - 4	4 5	8	17	25	2 20	04	+
9 - 8	2 4	8	9	17	1 37	2	—
10 - 9	1 8	3	8	11	80	.4	—
10 - 8	4 2	3	9	12	2 31	04	+
14 - 10	1 8	4	3	7	1 18	.3	—
17 - 10	2 3	2	3	5	61	6	—
21 - 17	3 4	23	2	25	79	4	—
21 14	3 9	23	4	27	1 22	2	—
21 - 10	5 7	23	3	26	1 60	1	—
21 - 19	4 3	23	4	27	1 28	2	—
20 17	5 1	4	2	6	1 34	2	—
20 - 14	5 6	4	4	8	2 82	02	+
22 - 14	6 1	65	4	69	2 36	02	+
22 17	5 6	65	2	67	1 64	1	—

Group 1 is found to be significantly different from group 2 or 4, the next lowest in mean site index. This group of xeric acid sands with weak A_2 horizon therefore may stand by itself, distinct from any of the other groups. The next significant difference is found between groups 9 and 4. At the same time, 8 and 4 and 9 and 8 are not significantly different insofar as the variability of the site indices is concerned. It appears then, on this basis, that groups 2, 3, 4, 5, and 6 could be combined, and that 7 and 8 might be placed either with this combination or with group 9. Group 10 and those above it are significantly different from 8 and those below, but 10 is not significantly different from 9. There is some doubt therefore whether 9 should be included with 7 and 8 or with 10 and 11. Above these, the groups form a rather gradually increasing series without marked differences up to 19, 20, and 22. These

three are significantly different from group 14 and those with site index lower than 14. Even 21 and 10 are not demonstrably different, and therefore all the intermediate groups, 11, 12, 13, 14, 15, 16, 17, and 18, may be considered as parts of a single grouping with respect to mean site index. This leaves a final grouping of 19, 20, and 22. On the basis of their variability therefore, the 22 groups could be condensed into 4 or possibly 6 classes which would have significant differences between but not within the groupings. However, this is a greater degree of condensation than is needed, and before it is accepted the groupings will be examined to see if widely and unreasonably diverse groups are being combined.

Some genetic relationship should exist to justify combining these soil groups, and such relationships may be seen most readily by referring to figure 12. In that cross-classification, soil groups along the same horizontal or along the same vertical element tend to be more closely related than those in different rows or columns. With this as a guide to logical relationships, the groupings indicated by lack of significant differences in mean site index may be reexamined. One of the objects sought is to establish 12 groupings of soil profiles, so that the correlation ratio for the 12 groups and the 230 samples may be compared with that for the texture-surface formation groups based on the same numbers, in order to avoid any discrepancy in the comparison which might be caused by the use of 12 and 22 groups respectively.

Group 1, the sands with weak A_2 on acid sandy subsoil, may be left as a single group. Out of the combination of groups 2 through 7, 3 and 4 are both xeric with poorly developed A_2 horizon and acid subsoils. Groups 4 and 5 are both on a noncalcareous rock substratum. There is therefore some genetic relationship and justification in a composite of groups 3, 4, and 5. Groups 2, 6, and 7 are related in that all three are on a clayey, calcareous, poorly drained parent material and therefore may logically be grouped. At the same time these three could not reasonably be combined with the preceding groups, although with respect to mean site index they are not significantly different. Group 8, xeric sands with weak A_2 horizon and acid sandy C horizon; group 9, wet, poorly drained soils with weak A_2 and clayey calcareous C horizon; and group 10, sandy loams with weak A_2 and clayey, noncalcareous C horizon, are genetically distinct and may be left as separate groups. A combination of groups 11 and 13 is based on the characteristics common to both—a glei horizon, strong A_2, and acid C horizon. Group 12 and 15 both have strong A_2, no glei, and sandy C horizon, so that they may logically be combined. Groups 14 and 17 form a composite, with poorly developed A_2 horizon and xeric environment in common.

This leaves only groups 16 and 18 out of the biometrically undifferentiated series from 11 through 18, and they are combined because both are wet soils with poorly developed A_2 and noncalcareous C horizon. Groups 19 and 20 are genetically related in having developed upon a more or less hydric sandy

calcareous parent material and are therefore combined. This leaves the final combination of groups 21 and 22, both with strong A_2 and no glei horizon on clayey subsoil.

The foregoing 12 composite groups were used for another calculation of correlation ratio between mean site-index and soil-profile groupings, with the essential figures and results shown in table 14. The figure of 0.788 for the correlation ratio between soil-profile groups and site index based on 12 classes is almost identical with that based on 22 groups (0.795) and is comparable with and superior to the value of 0.699 derived from the combined texture and surface-formation groups when correlated with site index. The significance of the difference between these two correlation ratios is indicated by the ratio of their difference to the standard deviation of that difference. Algebraically this is expressed as

$$\frac{\eta_1 - \eta_2}{\sqrt{\dfrac{\sigma^2\eta_1}{N_1} + \dfrac{\sigma^2\eta_2}{N_2}}}$$

The standard errors of the correlation ratios are determined from the relation

$$\sigma_\eta = \frac{1 - \eta^2}{\sqrt{N}}$$

This formula is based on the assumption, which is not strictly true, that the distribution of the correlation ratio is normal. However, when η and N are large, as in the present instance, the inaccuracy in the standard error from

TABLE 14. CORRELATION RATIO BETWEEN 12 SOIL-PROFILE CLASSES AND MEAN SITE INDEX

Soil-profile classes	Plots (n)	Mean site index (m_I)	$m_I - M_I$	$(m_I - M_I)^2$	$(m_I - M_I)^2 n$
	Number				
1	8	47.6	—14.9	222.0	1,776.0
3, 4, 5	36	54.9	— 7.6	57.8	2,080.8
2, 6, 7	14	55.6	— 6.9	47.6	666.4
8	10	56.8	— 5.7	32.5	325.0
9	9	59.2	— 3.3	10.9	98.1
10	4	61.0	— 1.5	2.3	9.2
11, 13	6	61.8	— 7	5	3.0
12, 15	33	62.0	— .5	3	9.9
14, 17	8	63.0	5	3	2.4
16, 18	2	65.0	2.5	6.3	12.6
21, 22	90	68.3	5.8	33.6	3,024.0
19, 20.	10	69.7	7.2	51.8	518.0
$\Sigma n (= N)$ ..	230				
$\Sigma[(m_I - M_I)^2 n]$	.			.	8,525.4

$$\sigma M_I = \sqrt{\frac{\Sigma[(m_I - M_I)^2 n]}{N}} = 6.09 \qquad \eta = \frac{\sigma M_I}{\sigma_I} = 0.788$$

$$\sigma_I = \sqrt{\frac{\Sigma I^2}{N} - M^2_I} = 7.74$$

$$M_I = 62.5$$

this cause is not likely to invalidate the use of the measure. For $\eta_1 = 0.788$ and $N = 230$, $\sigma_{\eta_1} = 0.025$. For $\eta_2 = 0.699$ and $N = 230$, $\sigma_{\eta_2} = 0.034$. Then, $\sigma_{\eta_1 - \eta_2} = 0.003$. The ratio of the difference, 0.089, to 0.003 is 30 so that the difference is unquestionably significant. The soil profiles therefore offer the most reliable basis of any of the soil groupings which have been tried for the classification of the habitats according to their productivity for the growth of aspen.

Before taking up a fifth classification of the habitats of the aspen community, based on the plant indicators, and comparing all five of them, it is necessary to consider in some detail the associated vegetation and the possibilities of its use for purposes of classification.

ANALYSIS OF ASSOCIATED VEGETATION

In several respects the plant indicators, including all the associated species found in the aspen community, are more difficult to treat satisfactorily in relation to habitat than are the soil and growth factors. In the first place there are 236 species which were recorded in the aspen community and from 10 to 50 of them were found on each plot. Each of these species has its own evolutionary adaptation and reaction to the different complexes of growth factors represented in the individual habitats. Unfortunately, some of the factors which influence the plants could not be eliminated or held constant, either as a whole or in the categories of a classification. Differences in light penetrating the aspen canopies of different densities unquestionably influenced the occurrence of certain species. The range of light intensities did not extend to complete sun and sky light, for plots were taken only where the aspen was sufficiently well represented to give character to the community and where it was at least 16 years old. The densities of the aspen canopy did, however, vary considerably, a fact which may underlie some of the variations between plots.

Some of the plant enumerations of individual plots are more or less incomplete owing to seasonal changes in the vegetation. Obviously, an examination in May will not reveal some of the late summer species, and September lists will not include all those of early spring. The frequencies of some of the distinctly seasonal species are doubtless too low for this reason. However, it does not seem likely that any considerable errors in the uses made of the records of associated vegetation will be incurred from this cause.

The vegetation is also influenced by the time which has elapsed since the last fire, which in the aspen community is one year more than the age of the dominant aspens. Areas were avoided where fire scars at the bases of trees indicated that fire had burned since the establishment of the aspen stand. The restriction of the sample areas to stands more than 15 years old allowed ample time for the aspen to have established its dominance, for the disap-

pearance of most of the transitory pioneers which follow fires, and for the attainment of a relatively slow rate of vegetational change.

Notwithstanding these facts there will evidently be differences in the plants between plots less than 30 years old and those over 50 years owing to the greater length of time for vegetational development. As the aspen stands grow older, invading species from the succeeding stages in the succession gradually become established and some of the relic species from the preceding stages disappear. The effect of these floristic changes associated with differences in the age of aspen is somewhat obscured by the presence of species supposedly characteristic of a later stage in the succession in young stands of aspen in company with pioneer species. This frequent occurrence is apparently due to the past fire history of the area. A hot fire which completely covered the area, or repeated fires at short intervals, eliminated relic species from previous forest stages except those which came up from the roots or underground parts which were not killed by the fires. In many places, however, the aspen started after a light fire which did not completely cover the area or kill all the pre-existing vegetation. In such cases, relic species are found in the aspen community from its inception in association with the pioneers which have started from light wind-borne seed, or from the underground parts of the previous generation. Actually a considerable number of the most common species in the community, such as Corylus and *Aralia nudicaulis*, belong to this latter group.

Admitting the varying influences of past fire history and age of the aspen on the composition and abundance of the different species in the associated vegetation, it would still be very difficult 16 to 85 years after the origin of the community to determine in each sample area how the individual species happen to be there. Moreover it is doubtful whether such a determination would do more than support the obvious statement that the older the aspen, the more frequently and commonly are found plants indicating a change in vegetation toward a succeeding stage in the natural succession.

The associated vegetation is analyzed by species according to the frequency of its occurrence in any particular group. The frequency is expressed numerically as the percentage which the number of occurrences in a group bears to the total number of plots in that group or in all groups. This is the "constancy" concept of Braun-Blanquet and Pavillard (1930), although it is hardly distinct in this use from the frequency or frequency percent of Raunkaier (1918), more commonly found in American literature. The indicator value of a species is not, however, always proportional to its frequency. Several of the species which have the highest frequencies are so universally present in all the habitats that they are almost valueless as indicators of habitat differences. At the other extreme a number of species with very low frequencies are found so rarely in the aspen community, that, even if their presence were proved to indicate rather specifically a certain habitat or group

TABLE 15. VEGETATION FREQUENCIES IN COMBINED TEXTURE-SURFACE FORMATION GROUPS

Species	Group Number											
	1	2	3	4	5	6	7	8	9	10	11	12
Abies balsamea	43		85	92	73	31	50	75	23	49	31	41
Acer rubrum	43	80	15	8	27	38	8	25		9	14	21
A. saccharum			10	25	9	19	25		.	14	14	20
A. spicatum			60	8	55		29		15	26	12	31
Actaea rubra		20	5							3		8
Alnus incana			40	42	36	19	17	50	31	11	19	16
Amelanchier spp.	14		25	50	27	13	21	50	15	26	17	30
Amphicarpa monoica				..		6	4			6		
Anaphalis margaritacea								..			2	
Anemone quinquifolia											2	7
Apocynum androsaemifolium						13			15	3		8
Aralia nudicaulis	14	20	85	33	73	19	50		54	43	33	61
Asarum canadense			3	8			4	25	23	6	7	13
Asplenium filix-femina			5				17			26	31	23
Aster macrophyllus	86	100	100	75	100	75	83	50	77	69	86	71
Betula lutea					9		17	25		3	2	
B. papyrifera	86	80	100	92	91	88	75	75	15	80	62	69
Caltha palustris										3		
Carex sp.								50		6		2
Carpinus caroliniana							4			3		
Carya cordiformis							4					
Chamaedaphne calyculata											2	
Chimaphila umbellata							8					
Circaea alpina												2
Clintonia borealis		20	60	33	64	6	50	25	31	46	19	44
Comptonia asplenifolia	57	20				13					5	
Coptis trifolia								25		3	2	2
Cornus canadensis	43	40	80	58	91	44	58	25	23	51	31	33
C. candidissima				8								
C. rugosa		20	15	8	27		21		77	23	38	38
C. stolonifera								75			2	2
Corylus rostrata	71	60	100	50	73	63	67	50	46	63	86	72
Crataegus rotundifolia											10	2
Cypripedium parviflorum											2	2
Diervilla lonicera	71	60	60	33	82	44	48	25	23	34	19	39
Dirca palustris							4					2
Epigaea repens			22	8	27	6	4		8			2
Epilobium angustifolium			25	42		19	4		54	9		5
Epipactis pubescens												2
Equisetum arvense			5	8	18		8	25	8	6	5	7
Fragaria virginiana	43	40	30	58	45	56	58	50	100	49	57	59
Fraxinus nigra							4	50		9	2	7
F. pennsylvanica var. *lanceolata*				17		6	8		8	9	21	25
Galium triflorum			30		9	19	4	25	85	14	12	43
Gaultheria procumbens	71	20				44	4		8	6	7	2
Geum virginianum												2
Gramineae	29	20		42		38	25	25	23	11	41	21
Hepatica triloba		20	5	17			4			11	2	16
Impatiens pallida			5		9						2	
Iris versicolor								25				
Juglans cinerea							1					
Larix laricina	14		10	8	9		8	50		3	5	3
Lathyrus ochroleucus } *L. venosus*	.	20	30	33	9	6	17		8	9	7	26
Ledum groenlandicum					9							
Linnaea borealis		.	25			6	4	50			5	
Lonicera canadensis			5	8	9				8	3	5	7
Lycopodium complanatum	14		20		18		8				2	
L. obscurum var. *dendroideum*	29		35	8	27	25	29		8	29	12	5
Maianthemum canadense	29	20	25		9	6	17	50	54	14	21	33
Melampyrum lineare	14		.			6						
Mitchella repens						6	8			3		
Mitella nuda			5					25	[illegible]		[illegible]	7
Nemopanthus mucronata	14				..		.					
Onoclea sensibilis												2
Osmunda claytoniana												7
Ostrya virginiana				[illegible]			8			9	2	3

Species	Group Number											
	1	2	3	4	5	6	7	8	9	10	11	12
Parthenocissus vitacea											2	
Pedicularis canadensis						6						
Petasites palmatus			10	25		6	13		15	11	2	15
Picea canadensis	43		75	92	55	31	46	25	8	40	17	23
P. mariana	43		35	25	36	13	21	25	8	17	12	8
Pinus banksiana	29		45	17	64	13	13			17	26	2
P. resinosa	71	60	35	42	27	44	25			11	26	5
P. strobus	100	80	60	67	55	87	42	23	8	29	33	25
Polygonatum biflorum			15		36		8			11	5	15
Populus balsamifera						6	4	25		6	2	15
Prunus americana										3	10	5
P. pennsylvanica	43	40	10	17	5	31	13	25	8	11	5	2
P. serotina	14	20				13	8			6	7	5
P. virginiana		40	15		36	6			38	31	19	39
Pteris aquilina	86	60	45	42	45	50	50	25	23	46	48	41
Pyrola elliptica			5	8			8			3	2	11
Quercus alba							8			3		
Q. borealis	29	20		17		38	13			14	10	7
Q. ellipsoidalis		20										
Q. macrocarpa		20				13	4		31	17	45	38
Rhus toxicodendron		20				6	4		23	3	7	7
Ribes cynosbati			5	8	9		8		15	11	5	18
R. triste								25				
Rosa blanda			40	33	36	19	25	25	85	31	17	39
Rubus argutus (?)	29		5	8	18	19	8			3	2	2
R. parviflorus			5	8	9		4		15		5	
R. pubescens			5				4	50	8	11	21	16
R. strigosus							4			3		7
Salix spp.	43	20	55	50	27	19	4	25		20	17	10
Sanguinaria canadensis										3		2
Sanicula marylandica												2
Smilacina racemosa							8		8		5	15
Sorbus americana			5		18		4		23	3		2
Sphagnum spp			5				4	50		3	5	3
Streptopus longipes	14		10		9	6			23	14	5	8
Taxus canadensis			5				4		8			
Thalictrum dioicum		20				13	13		23	20	43	51
Thuja occidentalis			33		9	6	13	50		6	7	2
Tilia americana				8			17		8	9	10	26
Trientalis americana			15		9		4	50	15	9	10	15
Trillium grandiflorum						6					2	8
Tsuga canadensis						6					5	
Ulmus americana						6	8		23	6	26	38
Uvularia grandiflora						13	4	25	8	3	5	16
Vaccinium pennsylvanicum	86	20	25	17	36	25	8			9	7	
Viburnum acerifolium												2
V. affine var. *hypomalacum*												10
V. lentago								25		3		3
V. trilobum												5
Viola spp.				8				25	23	3	2	10
Waldsteinia fragarioides	29	60				13	4		.			
Zanthoxylum americanum									..			2

of habitats, they would have little value in the characterization of those habitats. Certain species with intermediate frequencies are actually the most useful indicators of growth and habitat differences.

The plants associated with aspen either individually or in groups may be analyzed as dependent, when site index or habitat groups are used as the independent variable; or the plant groups may be used as the independent variable when they are combined in classes based upon the vegetation itself without regard to habitat. Both methods of analysis have been tried and will be discussed, when the plants are considered, first, as the dependent variable

with groupings of site index and soil, and second, as the independent variable.

As a matter of convenience for reference to individual species, and because phylogenetic relationships are of minor importance in relation to habitat and aspen growth, the lists of species are arranged in alphabetical order of the initial letters of the genera and of the species within a genus, except where the order of magnitude of their frequencies is an important consideration.

PLANT INDICATORS AND COMBINED SOIL TEXTURE AND SURFACE FORMATION GROUPS

The habitat groups based on the combination of soil texture and geological formation have been shown to be superior to either soil class or surface formation in relation to height growth of aspen, and the same superiority for the same reasons would undoubtedly appear in the relations to plant indicators. For that reason the two latter groupings have not been analyzed separately in relation to the associated vegetation. Moreover, it will appear from the analysis of the combined groups whether any significant relationships would be likely to be derived from the separate groups.

The frequencies or the percentages which the numbers of occurrences bear to the total number of plots in each soil group are shown in table 15. The most striking thing in this table is the fact that almost all of the common species are represented with high frequencies in almost all soil groups. In other words, the common species are not characteristic of any one soil group exclusively or even of any two or three related groups. In spite of this first and justifiable impression, there are differences in the magnitudes of the frequencies, and it will be worth while to consider each soil group separately to see which species, if any, can be considered at all characteristic. For this purpose, those species will be selected as characteristic which have the highest frequency in that group as compared with any other group, and those as common which have high frequencies in the group although not as high as in some other soil group. This use of the term "characteristic" does not correspond exactly to that of Braun-Blanquet and Pavillard (1930), who restrict it to certain degrees of exclusiveness of the occurrence of a species in different plant associations. Table 16 lists, for each of the 12 groups, the characteristic species arranged in descending order of their frequencies.

In this way it is possible to show an apparent significance of the different species as indicating certain soil groups. A part of the characteristic species do show a tendency on the average for many or very large areas of a given soil group to represent that group of habitats rather than any other. For any single sample area, however, the plants which may be found have very uncertain reliability in indicating the habitat group to which the area belongs. For example, on one plot belonging, according to the character of the soil and

TABLE 16. CHARACTERISTIC SPECIES OF 12 DIFFERENT SOIL GROUPS IN THE ASPEN COMMUNITY

Group 1. Sands and Fine Sands on Red-Drift Outwash (7 Plots)

Characteristic species	Frequency	Common species	Frequency
	Percent		*Percent*
Pinus strobus	100	*Betula papyrifera*	86
Vaccinium pennsylvanicum	86	*Aster macrophyllus*	86
Pteris aquilina	86	*Corylus rostrata*	71
Gaultheria procumbens	71	*Diervilla lonicera*	71
Pinus resinosa	71	*Prunus serotina*	14
Comptonia asplenifolia	57		
Picea mariana	43		
Prunus pennsylvanica	43		
Rubus argutus (?)	29		
Waldsteinia fragarioides	29		
Nemopanthus mucronata	14		

Group 2. Sandy Loams and Heavier Soils on Red-Drift Outwash (5 Plots)

Aster macrophyllus	100	*Betula papyrifera*	80
Acer rubrum	80	*Corylus rostrata*	80
Prunus virginiana	40	*Pinus strobus*	80
P. serotina	20	*Diervilla lonicera*	60
Actaea rubra	20	*Pinus resinosa*	60
Hepatica triloba	20	*Pteris aquilina*	60

Group 3. Red-Drift Fine Sands, Sandy Loams, and Loams on Rock (20 Plots)

Aster macrophyllus	100	*Abies balsamea*	85
Betula papyrifera	100	*Cornus canadensis*	80
Corylus rostrata	100	*Picea canadensis*	75
Aralia nudicaulis	85	*Clintonia borealis*	60
Acer spicatum	60	*Diervilla lonicera*	60
Salix spp.	55	*Pinus strobus*	60
Lycopodium obscurum var *dendroideum*	35		
L. complanatum	20		
Taxus canadensis	5		
Sphagnum sp	5		

Group 4. Clay Loams and Clays on Lake-Bed Clay (12 Plots)

Abies balsamea	92	*Betula papyrifera*	92
Picea canadensis	92	*Aster macrophyllus*	75
Amelanchier sp	50	*Pinus strobus*	67
Gramineae	42	*Cornus canadensis*	58
Lathyrus ochroleucus } *L. venosus* }	33	*Fragaria virginiana*	58
		Alnus incana	42
Acer saccharum	25		
Petasites palmatus	25		

Group 5. Red-Drift Fine Sandy Loams and Silt Loams on Rock (11 Plots)

Aster macrophyllus	100	*Betula papyrifera*	91
Cornus canadensis	91	*Abies balsamea*	73
Diervilla lonicera	82	*Aralia nudicaulis*	73
Clintonia borealis	64	*Corylus rostrata*	73
Polygonatum biflorum	36	*Acer spicatum*	55
Epigaea repens	27	*Picea canadensis*	55
Lonicera canadensis	9	*Pinus strobus*	55
Ledum groenlandicum	9	*Equisetum arvense*	18

Group 6. Sands on Sandy Moraine or on Lake-Washed Sandy Till (16 Plots)

Characteristic species	Frequency	Common species	Frequency
	Percent		*Percent*
Quercus borealis	38	*Betula papyrifera*	88
Populus grandidentata	6	*Aster macrophyllus*	75
Pedicularis canadensis	6	*Pinus strobus*	75
		Corylus rostrata	63
		Fragaria virginiana	56
		Pteris aquilina	50
		Cornus canadensis	44
		Gaultheria procumbens	44
		Pinus resinosa	44
		Diervilla lonicera	44

Group 7. Fine Sands and Red-Drift Sandy Loams on Sandy Moraine or on Lake-Washed Sandy Till (24 Plots)

Acer saccharum	25	*Aster macrophyllus*	83
Betula lutea	17	*Betula papyrifera*	75
Chimaphila umbellata var. *cisatlantica*	8	*Corylus rostrata*	67
Mitchella repens	8	*Cornus canadensis*	58
Carpinus caroliniana	4	*Fragaria virginiana*	58
Carya cordiformis	4	*Abies balsamea*	50
Dirca palustris	4	*Aralia nudicaulis*	50
Juglans cinerea	4	*Clintonia borealis*	50
Taxus canadensis	4	*Pteris aquilina*	50

Group 8. Peat (4 Plots)

Cornus stolonifera	75	*Abies balsamea*	75
Alnus incana	50	*Betula papyrifera*	75
Carex sp.	50	*Aster macrophyllus*	50
Fraxinus nigra	50	*Corylus rostrata*	50
Larix laricina	50	*Fragaria virginiana*	50
Linnaea borealis	50	*Maianthemum canadense*	50
Onoclea sensibilis	50		
Rubus pubescens	50		
Sphagnum sp.	50		
Thuja occidentalis	50		
Trientalis americana	50		
Betula lutea	25		
Coptis trifolia	25		
Equisetum arvense	25		
Iris versicolor	25		
Mitella nuda	25		
Populus balsamifera	25		
Ribes triste	25		
Viburnum lentago	25		

Group 9. Clay Loam on Lake-Washed Clayey Till (13 Plots)

Fragaria virginiana	100	*Aster macrophyllus*	77
Galium triflorum	85	*Aralia nudicaulis*	54
Rosa blanda	85	*Mitella nuda*	8
Cornus rugosa	77		
Epilobium angustifolium	54		
Maianthemum canadense	54		
Asarum canadense	23		
Rhus toxicodendron	23		
Sorbus americana	23		
Streptopus longipes	23		
Viola sp.	23		
Apocynum androsaemifolium	15		
Rubus parviflorus	15		
Taxus canadensis	8		

Group 10. Gray-Drift Sands and Red-Drift Sandy Loams and Fine Sandy Loams on Till, Clayey Moraine, or Lake-Washed Clayey Till (35 Plots)

Characteristic species	Frequency	Common species	Frequency
	Percent		*Percent*
Ostrya virginiana	9	*Betula papyrifera*	80
Amphicarpa monoica	6	*Aster macrophyllus*	69
Caltha palustris	3	*Corylus rostrata*	63
Sanguinaria canadensis	3	*Cornus canadensis*	51
		Lycopodium obscurum var. *dendroideum*	29

Group 11. Sandy Loams on Gray Drift and Fine Sandy Loams and Heavier Soils on Sandy Moraine or Lake-Washed Sandy Till (42 Plots)

Quercus macrocarpa	45	*Aster macrophyllus*	86
Asplenium filix-femina	31	*Corylus rostrata*	86
Prunus americana	10	*Betula papyrifera*	62
Crataegus rotundifolia	10	*Fragaria virginiana*	57
Tsuga canadensis	5	*Pteris aquilina*	48
Anaphalis margaritacea	2		
Cypripedium acaule	2		
Parthenocissus vitacea	2		

Group 12. Gray-Drift Sandy Loams and Fine Sandy Loams and Heavier Red-Drift Soils on Till, Clayey Moraine, or on Lake-Washed Clayey Till (61 Plots)

Thalictrum dioicum	51	*Corylus rostrata*	72
Ulmus americana	38	*Aster macrophyllus*	71
Tilia americana	26	*Betula papyrifera*	69
Fraxinus pennsylvanica var *lanceolata*	23	*Aralia nudicaulis*	61
Ribes cynosbati	18	*Fragaria virginiana*	59
Uvularia grandiflora	16	*Galium triflorum*	43
Smilacina racemosa	15	*Clintonia borealis*	44
Pyrola elliptica	11	*Prunus virginiana*	39
Viburnum affine var. *hypomalacum*	10		
Trillium grandiflorum	8		
Anemone quinquefolia	7		
Osmunda claytoniana	7		
Rubus strigosus	7		
Viburnum trilobum	5		
Sanicula marylandica	5		
Lathyrus venosus	3		
Circaea alpina	2		
Epipactis pubescens	2		
Geum virginianum	2		
Viburnum acerifolium	2		
Zanthoxylum americanum	2		

surface formation, to group 7, the following plants were found, each characteristic of the soil group indicated by number after the name:

Acer saccharum, 7
Aralia nudicaulis, 3
Aster macrophyllus, 2
Carex (pedunculata ?), 4
Betula lutea, 7
Cornus canadensis, 5
Diervilla lonicera, 5
Fragaria virginiana, 9
Mitchella repens, 7
Oryzopsis asperifolia, 4
Pinus strobus, 1
Polygonatum biflorum, 5
Populus grandidentata, 6
Pteris aquilina, 1
Pyrola secunda, 7
Quercus borealis, 6
Rubus (argutus ?), 1
Thuja occidentalis, 8
Tilia americana, 12
Tsuga canadensis, 11
Ulmus americana, 12
Viburnum acerifolium, 12

Summarizing by soil groups, group 7 has four characteristic species, groups 1, 5, and 12, three each, groups 4 and 6, two each, and groups 2, 3,

8, 9, and 11, one each. Group 7 to which the habitat belongs has a larger representation than any other, but all the rest of the 12 groups except number 10 are also represented. Not all the individual plots were analyzed in this way, but this example is believed to be quite representative of the loose nature of the relationship between individual plant indicator species and the texture-surface formation groups.

Some of the most common species in the aspen community are so nearly ubiquitous within the community that they are almost valueless as indicators of habitat differences. This may be noticed in the "common species" column of the preceding tabulations of several soil groups by the repeated appearance of certain species with high frequencies, notably, *Aster macrophyllus, Betula papyrifera, Corylus rostrata, Fragaria virginiana,* and others to a less extent. At the other extreme are the characteristic species with very low frequencies in many of the groups, which may be quite distinctive of that group but are found so rarely that little reliance can be placed upon them in assigning a given habitat to its proper group. Of course the chance of finding at least one of them becomes greater where there are several such species, as in group 12. On the other hand a species with a low frequency may actually be recorded as representative of a nontypical habitat within a group and thus have a small or even a deceptive indicator value. An example of this is afforded by the occurrence of *Nemopanthus mucronata* on one abnormally wet plot in group 1, although it can not be considered typical of the group 1 habitat.

Summarizing the relation between soil-texture and surface-formation groups and plant indicators, it may be said first that only a few of the low-frequency species are confined to, and therefore have specific indicator value for, a single habitat group. Second, the common species are too nearly ubiquitous in the aspen community to be used as indicators of habitat differences. Third, although there is a loose relationship, it is not sufficiently close to predict either the habitat group from the plants present or the plants from the habitat group.

Plant Indicators and Soil Types and Soil-Profile Groups

The foregoing rather unsatisfactory correlation between plant indicators and soil-texture and surface-formation groups may be extended by analogy to the relationships with soil types and profile groups. In that case, however, instead of 12 groups, there are 54 soil types and 22 profile groups. These narrower groupings representing more unified and homogeneous habitat conditions might appear, at first thought, to provide just what is needed for a close correlation with specific plant indicators. But, even with only 12 broad habitat categories, it was found that almost all of the plants occurred on several if not all of the soil groups. This is in agreement with the well-known fact that every plant is able to adapt itself to a considerable range of environmental variations. If, then, the 12 broad groups are not sufficiently comprehensive

to include the range of variations for most of the species, it is less likely that the narrower groups of 22 and 54 classes would encompass them. The data support this supposition. Almost every species which occurred on more than one or two plots also represented more than one soil type, and most of them more than one profile group. *Abies balsamea* for example was found on 45 of the 54 soil types, *Acer spicatum* on 28, and even a species of rather restricted habitat, *Larix laricina*, on 13. The same conclusion is applicable here that was arrived at above, namely, that the correlation between plant indicators and soil types or soil-profile groups is not sufficiently close to enable prediction of either one from the other.

The proof of the degree of correlation by biometric methods where 230 species and 54 soil types or even 22 profile groups are concerned would require many times the number of plots which were obtained in this study. If the species and groups or types are combined into a 6-by-6-fold classification, as they will be in a later and slightly different connection and as they have to be for the calculation of the contingency coefficient with the limited material available, the groups become so broad that they lose some of their significance as representing the relation of species to soil types.

NATURAL COMMUNITY PLANT-INDICATOR GROUPS

Whereas the vegetation has thus far been grouped according to predetermined habitat classes, the plant indicators will now be made the independent variable, and groups will be established on the basis of the natural community relations of the plants themselves irrespective of habitat or aspen growth. The communities in the region on habitats like those occupied by aspen have usually been characterized by the predominating tree growth. Using this as a starting point, lists of species of the aspen community also found in each of these other forest communities or types were compiled partly from the writer's own field notes, partly from manuscript notes of others, and partly from published references. For this purpose material from eastern Wisconsin and Michigan was used although it was somewhat outside the area from which the aspen material came. This disadvantage is considered to be outweighed by the advantage of having a larger number of sample areas upon which to base frequency percentages.

The compilation gives the following total numbers of lists or sample areas in each of the communities: Jack pine, 57; Norway pine, 9; white pine, 123; oak, 87; white spruce-balsam, 6; sugar maple, 24; ash-elm, 1; white cedar, 4; tamarack, 3; black spruce, 4; hemlock, 8; and alder-sedge, 3. These numbers are used as the denominators of the fractions for the frequency ratios, the actual numbers of occurrences of each species in a given community forming the numerators.

Each species is then considered to be characteristic of the community in which it has the highest frequency. This corresponds to the concept of Braun-

Blanquet and Pavillard (1930) who include as "characteristic" species those with exclusiveness indices of 5, 4, and 3 in a scale of 5. The characteristic species determined similarly by a percentage scale for each of the foregoing communities are listed below. If a species has equal frequencies in two communities it is included in both of them. Because of the small number of sample areas and the consequently inadequate representations of plants in a few of the communities, they were combined. Thus the alder-sedge was combined with the ash-elm, hemlock with sugar maple, and black spruce with tamarack, making nine communities in all.

Sugar maple community

Actaea rubra
Adiantum pedatum
Allium tricoccum
Amphicarpa monoica
Aralia nudicaulis
A. racemosa
Arisaema triphyllum
Asarum canadense
Aspidium noveboracense
A. spinulosum var. *intermedium*
Asplenium filix-femina
Betula lutea
Botrychium virginianum
Brachyelytrum erectum
Carex brunnescens
C. laxiflora var. *latiflora*
Carpinus caroliniana
Carya cordiformis
Caulophyllum thalictroides
Celastrus scandens
Circaea alpina
Clintonia borealis
Cornus alternifolia
C. rugosa
Corylus rostrata
Crataegus rotundifolia
Desmodium grandiflorum
Dioscorea villosa
Dirca palustris
Equisetum arvense
Fagus grandiflora
Galium aparine
G. asprellum
G. triflorum
Geranium bicknellii
Geum virginianum
Hystrix patula
Juglans cinerea
Lonicera canadensis
L. hirsuta
Luzula campestris var. *multiflora*
Lycopodium annotinum
L. lucidulum
Mitchella repens
Mitella diphylla
Osmunda cinnamomea
Osmorhiza claytoni
O. claytoniana
Ostrya virginiana
Parthenocissus vitacea
Phegopteris dryopteris
P. polypodioides
Phryma leptostachya
Polygonatum biflorum
Prunella vulgaris
Prunus americana
Pyrola elliptica
Quercus borealis
Q. macrocarpa var. *olivaeformis*
Ribes cynosbati
Rubus parviflorus
R. pubescens
Sambucus pubens
Sanguinaria canadensis
Smilacina racemosa
Smilax hispida
Streptopus longipes
Thalictrum dioicum
Tiarella cordifolia
Tilia americana
Trillium grandiflorum
Tsuga canadensis
Uvularia grandiflora
Viburnum lentago
Viola pubescens
Vitis vulpina

Ash-elm community

Acer rubrum
Alnus incana
Caltha palustris
Carex spp.
Cicuta maculata
Cornus stolonifera
Cryptotaenia canadensis
Epilobium palustris
Eupatorium purpureum
Fraxinus pennsylvanica var. *lanceolata*
F. nigra
Gramineae spp.
Ilex verticillata
Impatiens pallida
Iris versicolor
Juncus (tenuis?)
Onoclea sensibilis
O. struthiopteris
Smilacina stellata
Smilax herbacea
Populus balsamifera
Rudbeckia laciniata
Scutellaria lateriflora
Ulmus americana
Viburnum trilobum

Tamarack-black spruce community

Aspidium cristatum
Chamaedaphne calyculata
Chiogenes hispidula
Coptis trifolia
Cypripedium parviflorum
Epipactis pubescens
Larix laricina
Ledum groenlandicum
Mitella nuda
Picea mariana
Ribes prostratum
R. triste
Sphagnum spp.
Vaccinium canadense

White spruce-balsam community

Abies balsamea
Acer spicatum
Clintonia borealis
Cornus canadensis
Epipactis pubescens
Linnaea borealis
Lycopodium obscurum
var. *dendroideum*
Mertensia paniculata
Mitella nuda
Picea canadensis
Sorbus americana
Taxus canadensis
Trientalis americana
Viola renifolia

Jack pine community

Amelanchier laevis
Anaphalis margaritacea
Antennaria neodioica
Apocynum androsaemifolium
Aster ericoides
A. lindleyanus
Corylus americana
Diervilla lonicera
Lathyrus ochroleucus
L. venosus
Melampyrum lineare
Nemopanthus mucronata
Oryzopsis pungens
O. asperifolia
Pedicularis canadensis
Physalis lanceolata
Pinus banksiana
Polygala pauciflora
Rosa blanda
Rubus argutus
Salix humilis
Spiranthes gracilis
Steironema ciliata
Veronica virginiana
Viola conspersa
Waldsteinia fragarioides

Norway pine community

Anemone virginiana
Aster cordifolius
A. laevis
Chimaphila umbellata
var. *cisatlantica*
Cladonia spp.
Epigaea repens
Epilobium angustifolium
Fragaria virginiana
Galium boreale
Gaultheria procumbens
Habenaria orbiculata
Lycopodium complanatum
Oakesia sessiliflora
Pinus resinosa
Populus grandidentata
Prenanthes alba
Prunus pennsylvanica
Pyrola secunda
P. americana
Quercus alba
Sanicula marilandica
Symphoricarpos albus
Viburnum acerifolium
Vicia americana

White pine community

Anemone quinquefolia
Aquilegia canadensis
Aster macrophyllus
Geranium maculatum
Hepatica triloba
Lonicera dioica
var. *glaucescens*
Maianthemum canadense
Mitella diphylla
Monarda mollis
Pinus strobus
Potentilla sp.
Prunus serotina
P. virginiana
Pyrola americana
Ranunculus sp.
Rhus toxicodendron
Rubus strigosus
Trillium cernuum
Viburnum affine
var. *hypomalacum*
Zanthoxylum americanum

Oak community

Aronia melanocarpa
Carex (umbellata?)
Comptonia asplenifolia
Convolvulus spithamaeus
Corallorhiza striata
Cornus candidissima
Hammamelis virginiana
Helianthus divaricatus
Lysimachia quadrifolia
Pteris aquilina
Quercus ellipsoidalis
Solidago spp.
Vaccinium pennsylvanicum

White cedar community

Betula papyrifera	*Petasites palmatus*	*Thuja occidentalis*
Lycopodium clavatum		

The foregoing lists do not pretend to be complete for the communities represented and they do not necessarily include the most common species in those communities, but they are believed to show the communities other than aspen with which the species of the aspen community are most frequently associated. With these lists as a guide, the species recorded on each aspen plot were allocated to one of these groups and the plot assigned to that group which had the largest representation of species. This process resulted in a division of the aspen plots into 9 groups, which are called natural community groups. Three of these, sugar maple, white spruce-balsam, and white pine, had large representations of plots in comparison with the other six groups. These three groups were then subdivided according to the community represented by the second largest number of species. Thus, within the white spruce-balsam group, those plots which by the plant indicators showed relationship to jack pine or to Norway pine communities were separated from those which had plants chiefly representative of the sugar maple community. In the same way the white pine group was divided into four parts, white pine with jack pine indicators, white pine with white spruce-balsam indicators, white pine with sugar maple indicators, and white pine with tamarack-black spruce-cedar-ash indicators. Similarly the sugar maple group was subdivided into four, one with Norway pine indicators, one with white pine, one with white spruce-balsam, and the fourth with swamp species indicators.

In all this process of grouping and subdivision, it was evident that hardly one of the plant indicators was exclusively confined to any one group. Only the different frequencies of species in different groups served to differentiate between them by means of the associated vegetation. Often the small differences in frequency seem to offer only slight support for distinctions between plots and their allocation to groups; but in the aggregate they seem to have considerable significance, as will appear in the subsequent analysis of the relations of these groups to growth and soils.

The groups also have rather definite successional relations among themselves if it is assumed that the indicator plants have the same successional significance in the aspen community that they would have in the forest communities by the names of which they have been designated. The subdivision of the groups is somewhat finer than that ordinarily used in describing the stages in the succession in the region, and thus a part of them may be thought of as transitions between the usual stages. Furthermore the region happens to be partly in the zone of overlap between the sugar maple-basswood and the spruce-balsam-birch climaxes so that transitions between the two successions as well as between the stages in each one of them are represented.

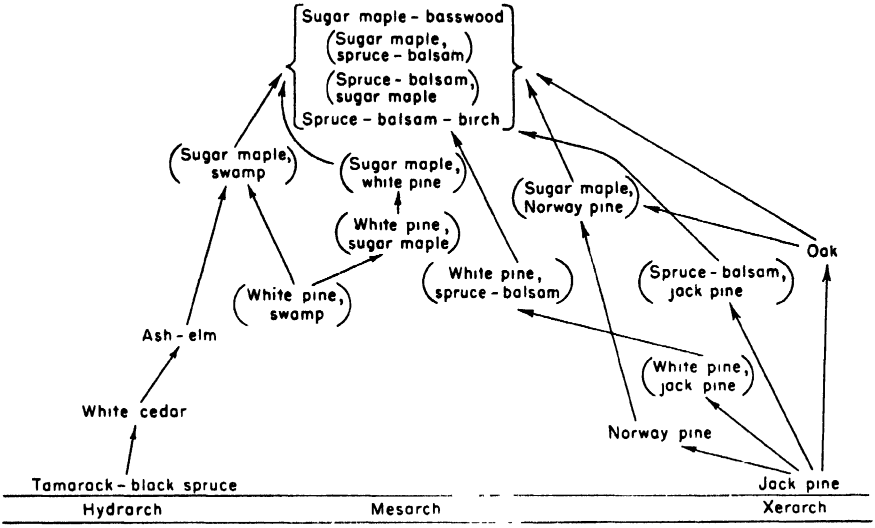

FIG. 14. Successional tendencies in natural community groups of aspen plant indicators. Parentheses indicate transitional stages.

The relation of each of the 16 groups to the successional diagram for the region is shown in figure 14. Evidence in the form of invading and relic species of the trees themselves is available in these plots in support of the relations shown, but it is not sufficiently relevant to the present subject to justify the lengthy presentation that would be required. The pioneer stages preceding the tree stages in the successions and those not represented in the data from the aspen community are omitted from the diagram.

If these groups are arranged as nearly as possible in ascending order of the successional stages toward the climaxes, combining the xerach and hydrarch stages in the same ascending scale, their sequence would be that of the first column in the following tabulation:

Successional sequence	*Site-index sequence*
1. Tamarack-black spruce	1. Norway pine
2. Jack pine	2. Tamarack-black spruce
3. Norway pine	3. White cedar
4. White cedar	4. Jack pine
5. White pine, jack pine	5. Spruce-balsam, jack pine
6. Oak	6. White pine, jack pine
7. Ash-elm	7. White pine, spruce-balsam
8. White pine, swamp	8. Oak
9. Spruce-balsam, jack pine	9. Spruce-balsam, maple
10. White pine, spruce-balsam	10. White pine, swamp
11. White pine, maple	11. Maple, Norway pine
12. Maple, Norway pine	12. Maple, white pine
13. Maple, white pine	13. White pine, maple
14. Maple, swamp	14. Maple, spruce-balsam
15. Spruce-balsam, maple	15. Maple, swamp
16. Maple, spr.:ce-balsam	16. Ash-elm

Obviously the relative positions of any two adjacent groups cannot be determined exactly and might be reversed, but roughly this order represents that of the natural succession. As a corollary, then, it should also represent a series of habitats in which each successive one has been built up by the addition of humus toward a more mesic and favorable environment until a later stage of more exacting species can invade and gain possession. If this be true, then it should follow that the foregoing order of groups should be that of increasing favorableness with respect to site index and growth of aspen. It will be interesting shortly to make the comparison, although it may be noted at this point that the ascending order of favorableness for the stages of natural succession would not necessarily for that reason be identical for the growth of aspen, a single community which normally takes its place as a pioneer tree stage of the mesarch succession.

The mean site indices for each of these 16 natural community plant-indicator groups were computed in the usual way. The values in ascending order determine the arrangement of groups in the site-index sequence, so that comparisons of the two sequences may be made. The larger discrepancies in the two sequences are represented by the noticeable differences in position of the spruce-balsam, jack pine; white pine, spruce-balsam; spruce-balsam, maple; and ash-elm. Apparently the wet conditions of habitat of the last community, or rather of the plants associated with the community, are favorable for the growth of aspen, notwithstanding the fact that they are more hydric than mesic and some distance removed from the climax habitat.

The other three groups are all characterized by the presence of large proportions of the species associated with the white spruce-balsam group. Furthermore, they are all three decidedly lower in the site-index sequence than in the successional sequence. This suggests that the white spruce-balsam, although it is a climax community, represents relatively unfavorable conditions for the growth of aspen in comparison with those of the maple climax. This might have been predicted from a consideration of the comparative distribution and environmental conditions of the two climaxes. The spruce-balsam is the northern conifer-forest climax associated with the cold climate, short growing season, and less favorable edaphic conditions of latitudes chiefly north of the United States. Within this region, the habitats which it occupies would naturally be less favorable than those with locally warmer climate, longer growing season, and more favorable soil-forming processes of the deciduous forest climax, here near its northern limit. If then the groups with spruce-balsam indicator plants were placed lower in the successional order than those with maple indicators, the series arranged according to the natural succession would correspond more closely with that determined by the mean site index of the aspen. On the whole there is a decided indication that, as the stages of natural succession, distinguished by the plant indicators, ap-

proach the climax, the habitats as measured by the growth of aspen are progressively more productive.

CORRELATION WITH SITE INDEX AND DIFFERENTIATION OF NATURAL COMMUNITY GROUPS

With these plant-indicator groups, it is now possible to calculate the correlation ratio with site index as the dependent variable, in the same way that similar measures were obtained with the groups based on soil or geological features. The present groups, however, have been established independently of soil characteristics except as the soils may have indirectly influenced the frequencies of the plants. The groups, arranged in ascending order of mean site index, are shown in table 17, with the essential figures for the computation of the correlation ratio.

TABLE 17. CORRELATION RATIO BETWEEN NATURAL COMMUNITY PLANT-INDICATOR GROUPS AND SITE INDEX

Plant-indicator group	Plots (n)	Mean site index (m_I)	$m_I - M_I$	$(m_I - M_I)^2$	$(m_I - M_I)^2 n$
	Number				
1. Norway pine ..	23	52 1	—10 8	116 6	2,681 8
2. Tamarack-black spruce	10	53 0	— 9 9	98 0	980 0
3 White cedar..	7	55 1	— 7 8	60.8	425 6
4. Jack pine	9	55 4	— 7 5	56 3	506 7
5 Spruce-balsam, jack pine	27	58 0	— 4 9	24 0	648 0
6. White pine, jack pine	12	58 5	— 4 4	19 4	232 8
7. White pine, spruce-balsam	5	59 2	— 3 7	13 7	68.5
8. Oak .	4	62 8	— 1	01	0
9. Spruce-balsam, maple	39	63 4	5	25	9 9
10. White pine, swamp	8	63 9	1 0	1 0	8 0
11. Maple, Norway pine	7	65 4	2 5	6 3	44 1
12. Maple, white pine	26	67 5	4 6	21 2	551 2
13. White pine, maple	16	67 8	4 9	24 0	384 0
14. Maple, spruce-balsam . .	6	68 8	5 9	34 8	208 8
15. Maple, swamp .	35	69 0	6 1	37 2	1,302 0
16. Ash-elm . . .	25	69 6	6 7	44 9	1,122.5
$\Sigma n (= N)$	259				
$\Sigma[(m_I - M_I)^2 n]$				.	9,173 9

$$\sigma_{M_I} = \sqrt{\frac{\Sigma[(m_I - M_I)^2 n]}{N}} = 5\ 95 \qquad \eta = \frac{\sigma_{M_I}}{\sigma_I} = 0.761$$

$$\sigma_I = \sqrt{\frac{\Sigma I^2}{N} - M_I^2} = 7\ 82$$

$$M_I = 62.9$$

The correlation ratio of 0.761 shows a considerable degree of relationship between site index and the plant-indicator groups. In other words, the natural community groups have a real value in the prediction within limits of the average site index or growth of the aspen. In comparison with the correlation ratios between site index and the soil groups, this one is distinctly higher than the 0.699 for combined texture and surface-formation groups but not very different from the 0.788 of the soil-profile groups. The difference

between 0.788 and 0.761 may be tested for significance in the same way that 0.788 has been shown to be significantly different from 0.699. The standard error of 0.788 is 0.025 as before. For 0.761 and N of 259, σ_η is 0.026. Then, the standard deviation of the difference is 0.0023 and the actual difference, 0.027, is twelve times this figure, making the correlation ratio with soil-profile groups significantly higher than that with plant-indicator groups. Thus the plant-indicator groups are only slightly inferior to the soil-profile groups as a basis for the differentiation of habitats with respect to their productivity for the growth of aspen.

Having determined the correlation, it will now be interesting to see whether the individual plant-indicator groups are significantly different one from another as judged by the variability of the site-index values within the single groups and, if not, which ones may be combined. Figure 15 shows the distributions of site-index values for each group and table 18 contains the figures for the calculation of the significance of differences.

Groups 1, 2, 3, and 4 may be combined insofar as their variability is concerned because 1 and 4, the extremes, are not significantly different. Group 5 is significantly different in mean site index from group 1 and is therefore considered to belong to a second combined grouping. Group 9 is the first one above 5 which is significantly different from it; wherefore groups 5, 6, 7, 8, and 9 may be combined. However, since 9 is significantly different from 6 and there is a noticeable gap between 7 and 8, two combined groupings were adopted, one including numbers 8, 9, and 10, and the other, 5, 6, and 7. Group 12 is significantly different from 9, although not from 10, and 16 is significantly different from 10, although not from 12. Evidently then, groups 12, 13, 14, 15, and 16 may be combined, leaving only the question of whether 11 should be placed with this group or with 8, 9, and 10. To sum up, the biometrically significant differences between these plant-indicator groups would not distinguish more than four groupings.

Is there any biological basis for these groupings? In the first 4 groups,

TABLE 18. SIGNIFICANCE OF DIFFERENCES BETWEEN MEAN SITE-INDEX VALUES OF NATURAL COMMUNITY PLANT-INDICATOR GROUPS

Group	$M_{I_2} - M_{I_1}$	n_2	n_1	n	t	P	Significance of difference
4 - 1	3 3	8	22	30	0.96	0 3	—
5 - 1	5 9	26	22	48	3.55	01	+
7 - 4	3 8	4	8	12	.61	.5	—
7 - 3	4.2	4	6	10	1 39	.2	—
8 - 7	3.6	3	4	7	1.55	.2	—
8 - 5	4 8	3	26	29	1.59	1	—
9 - 5	5 4	38	26	64	3.75	01	+
9 - 7	4.2	38	4	42	1 59	.1	—
9 - 6	4.9	38	11	49	2.73	.01	+
12 - 9	4.1	25	38	63	2 99	.01	+
12 - 10	3 6	25	7	32	1.59	.1	—
16 - 12	2.1	24	25	49	1 35	.2	—
16 - 10	5 7	24	7	31	2 20	.03	+

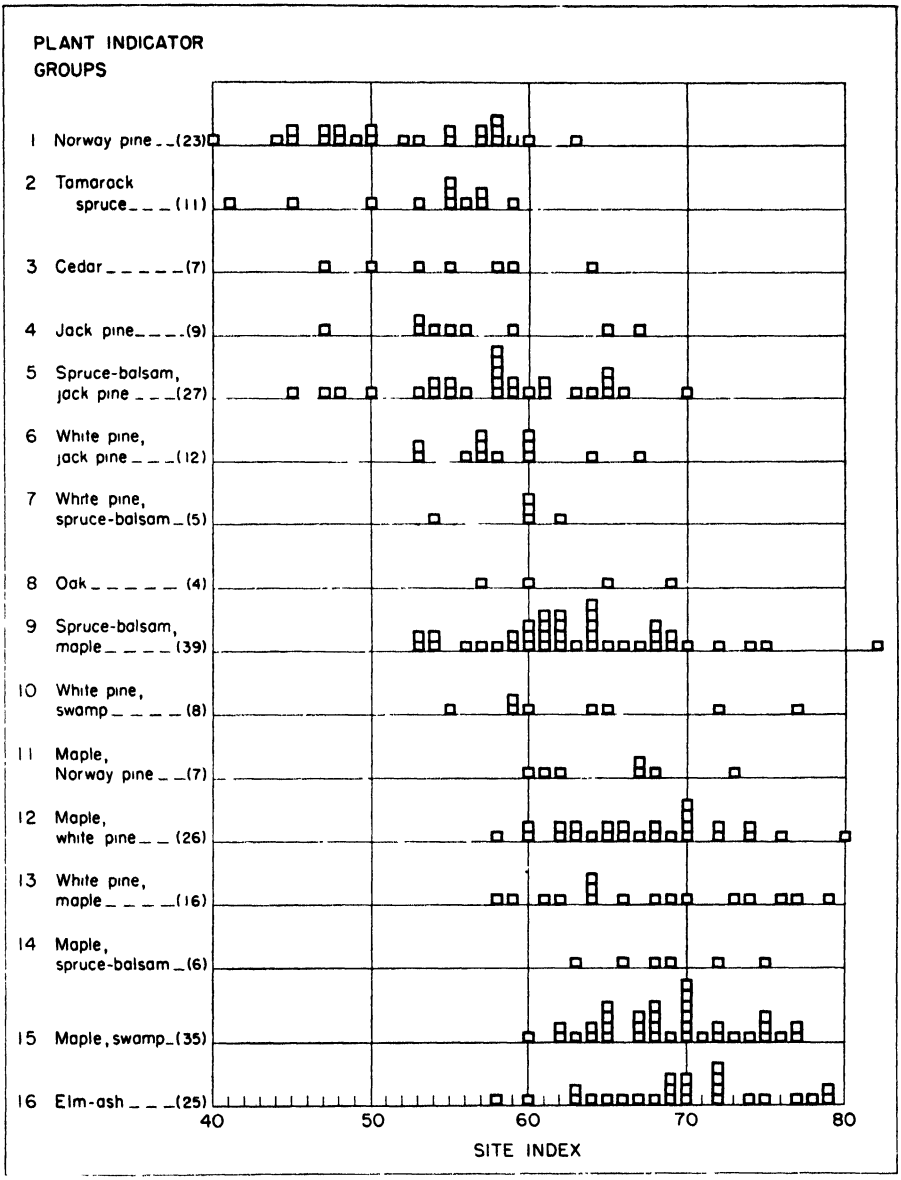

FIG. 15. Distribution of site indices by plant-indicator groups.

that of Norway pine may logically be combined with jack pine and tamarack-black spruce with white cedar, but there is no reason for combining the first two with the last two except that they happen to have closely corresponding values of the mean site index for aspen. Groups 5, 6, and 7 have sufficient similarities in their composition so that their combination does not violate the

usual ideas of relationship. Groups 8, 9, and 10 contain rather diverse elements and little biological justification can be adduced for their combination. Groups 11 through 16, with the exception of 16, have the sugar maple associates strongly represented in their composition, which gives them a degree of biological unity. Group 15, sugar maple, swamp is also related to the ash-elm group so that all six groups have some biological homogeneity. On the whole, the plant indicator-site index analysis, in respect to the number of significantly different groupings which it distinguishes, is not noticeably different from the soil groupings, about four being differentiated in each case; and, in this as in the previous analyses, these do not have complete physical or biological homogeneity.

RELATIONS OF PLANT-INDICATOR GROUPS AND SOIL-PROFILE GROUPS

There are 16 plant-indicator groups and 22 soil-profile groups in the classifications which seem to have the greatest biological unity. There would thus be 352 cells or categories in a cross-classification with these two series as variables. With only 265 plots, the use of such a degree of refinement disperses the data too thinly for an adequate measure of the relationship to be obtained. If the number of soil-profile groups is reduced to 11, however, the same that were used in the second determination of the correlation with site index, except that the two small groups 16 and 18 and 19 and 20 have been combined into one, some indication of the relation between the two groupings may be obtained. The numbers of plots in each of the cells of such a cross-classification are shown in figure 16. Evidently the distribution is not uniform. There is a noticeable concentration in the upper left-hand and a more significant one in the lower right-hand cells. This tendency may be interpreted roughly by the statement that, as the habitats classified by the soil profiles become more favorable, the frequency of occurrence of aspen plots increases from those characterized by the xeric and hydric to those with mesic or hydromesic plant indicators, chiefly sugar maple associates.

For the calculation of a biometric measure of the degree of association between these two nonquantitative series, a further concentration of the groups becomes necessary. For the determination of the coefficient of contingency, the material does not justify more than a 6-by-6-fold classification. Accordingly the plant-indicator groups and the soil-profile groups of figure 16 were further combined into six categories each, on the basis of the biological and genetic relationships, respectively. For the plant groups, numbers 1, 4, and 8, Norway pine, jack pine, and oak were combined as representing the three most xeric communities. Groups 2 and 3, tamarack-black spruce and white cedar, together form the most hydric group. Groups 5, 6, and 7 may be considered a white pine-white spruce-balsam-jack pine grouping with a certain degree of homogeneity. Groups 9 and 10, white spruce-balsam-maple and white pine-swamp, occupy somewhat similar hydro-mesic habitats and have a

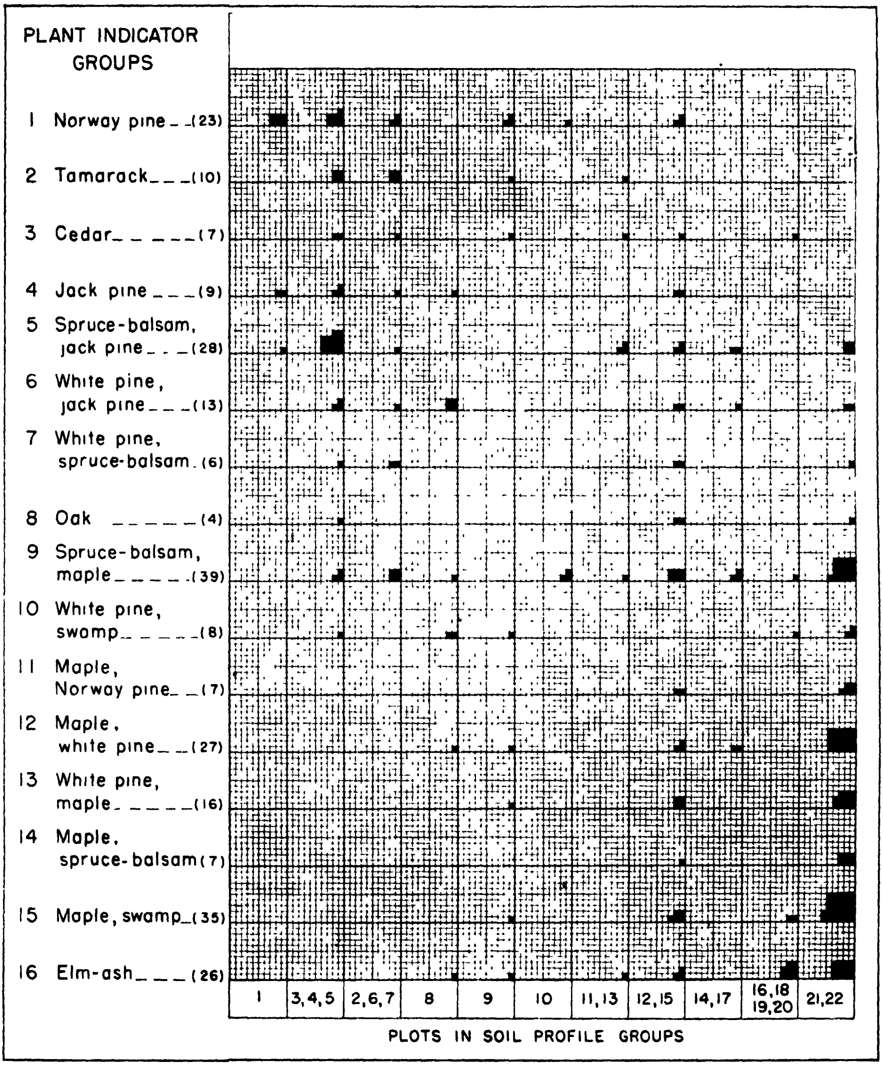

FIG. 16. Distribution of plots by plant-indicator and soil-profile groups.

number of species in common, associated particularly with *Abies balsamea*. Groups 11, 12, and 13 are the sugar maple-white pine-Norway pine transitions preceding the climax. The sixth grouping is composed of numbers 14, 15, and 16, the sugar maple-spruce-balsam, sugar maple-swamp, and ash-elm, the deciduous climax and the two groups most closely related to it in the hydric succession.

Similarly, for the soil-profile groups numbers 1, 3, 4, 5, and 8 form a combination of xeric soils on sandy or rock parent material, generally non-

calcareous with weak A_2 horizon. Groups 2, 6, 7, and 9 are poorly drained soils on clayey calcareous subsoil. Groups 10, 14, and 17 include the remaining groups with weak A_2 horizon not included in the first combination. Numbers 12 and 15 are characterized in common by a strongly developed A_2 horizon without a glei horizon on sandy parent material. The combination of groups 11, 13, 16, 18, 19, and 20 includes all the glei and hydric soils on sandy or noncalcareous clayey subsoils. The sixth and last grouping of numbers 21 and 22 includes the largest number of soil types, but all of them are characterized by strong A_2 horizons, without glei, on clayey parent material.

In combining the soil-profile and plant-indicator groups into these less numerous categories, something of homogeneity in the resulting groupings has evidently been sacrificed. From this point of view the process is undesirable and tends to obscure biological and physical differences. At the same time, however, in connection with the analyses of site-index relations with these two classifications, it has been shown that the differences between the individual groups are in many instances not significant biometrically. The differences between the nonquantitative groups cannot be determined in the same way. If they could be, it seems likely that the same paucity of significant differences in the 16 and 22 or 12 group classifications would be found. It has been pointed out that the 16 plant-indicator groups include transitional stages between those usually recognized in successional studies. On the whole, therefore, it is not improbable that the 6-by-6 classification may approximate the number of groupings which are really distinguishable and useful. Even if this is not wholly true and the broader groupings partially fail to differentiate between distinct categories, it does not necessarily follow that the 6-by-6 classification will not give a reliable indication of the degree of relationship between soil-profile and plant-indicator groups. As direct evidence, it may be recalled that the change from 22 to 12 soil-profile groups in the correlation ratio with site index changed the value only from 0.795 to 0.788. In any case it will be interesting to see what degree of association between the two series of six categories each is indicated by the coefficient of contingency. The essential figures and the method of calculation, adapted in part from Yule (1924), are given in table 19.

The probability of less than 0.01 may be interpreted to mean that the difference between the actual and the computed distributions is significant. The contingency coefficient of 0.62 indicates a significant degree of association. The maximum possible value of the coefficient for a 6-by-6-fold table is 0.913, which would be obtained if all the plots were concentrated in the diagonal row of cells from upper left-hand to lower right-hand corner of the table. The conclusion previously suggested is, therefore, confirmed that the soil-profile and plant-indicator categories are distinctly associated.

In the upper section of table 19, there is a simultaneous progression from

TABLE 19. COEFFICIENT OF CONTINGENCY AS DEVELOPED FROM SOIL-PROFILE GROUPINGS AND PLANT-INDICATOR CLASSES

DISTRIBUTION OF PLOTS BY NUMBER

Plant-indicator classes	Soil-Profile Groupings						
	1,3,4, 5,8	2,6,7,9	10,14,17	12,15	11,13,16, 18,19,20	21,22	n_p
1,4,8	20	7	1	7	0	1	36
2,3	6	7	C	1	3	0	17
5,6,7	23	4	3	7	3	7	47
9,10	7	5	6	6	3	20	47
11,12,13	1	2	2	9	0	36	50
14,15,16	1	2	0	9	11	45	68
n_t	58	27	12	39	20	109	
N							265

DISTRIBUTION COMPUTED ACCORDING TO TOTALS $= \frac{n_t \cdot n_p}{N}$

1,4,8	7 9	3 7	1 6	5 3	2 7	14 8	36 0
2,3	3 7	1 7	8	2 5	1 3	7 0	17 0
5,6,7	10 3	4 8	2 1	6 9	3 5	19 3	46 9
9,10	10 3	4 8	2 1	6 9	3.5	19 3	46 9
11,12,13	10 9	5 1	2 3	7 3	3 8	20 6	50 0
14,15,16	14 9	6 9	3 1	10 0	5 1	28 0	68 0

$$S = \Sigma \left[\frac{n^2{}_{pt}}{\frac{n_t \cdot n_p}{N}} \right] = 427\ 7 \qquad \chi^2 = S - N = 162.7$$

Number of degrees of freedom, $5 \times 5 = 25$. $P = 0\ 01 -$

$$C = \sqrt{\frac{S - N}{S}} = 0\ 62$$

left to right and from top to bottom in the soil groups, from the immature, less well-developed and less favorable soils to the mature, well-developed and more favorable soils; and in the vegetation groups, from the early successional stages, both xeric and hydric, to the hydro-mesic subclimax and mesic climax species. The parallelism in the genetic development of the soils and the successional development of the vegetation is marked and is the more noteworthy because the concepts of the dynamic processes of soil formation, of immaturity and maturity, have been evolved independently of the similar concepts in vegetational succession. Inasmuch as the sample plots come from different habitats and do not actually represent the changes in soil and vegetation with time on identical areas, it would be unjustifiable to conclude that the two processes go on step by step and at the same rate. Nevertheless the suggestion is interesting that, given a certain stage in soil formation as indicated by the profile, the species of a corresponding stage in vegetational succession tend to be associated with it. Furthermore, it seems likely that each one of the two processes is influenced in its rate of development by the other.

One further consideration tends to confirm this suggestion. Both plant-indicator and soil-profile groups have been shown to have moderately high correlations with site index. The ascending order of the groups in each of these correlations is indicated approximately by their numerical designations. In table 19, it may be noticed that the numbers of the soil-profile groups increase from left to right and of the plant-indicator groups from top to bottom, the same directions which result in the contingency trend. This affords additional evidence of the association between soil-profile and plant-indicator groups.

RELATIONS OF INDIVIDUAL PLANT INDICATORS AND SITE INDEX

The simplest and most obvious way in which to use plant indicators is as individual species whose presence, absence, or frequency may be found to represent some condition of habitat or growth. The value of individual species as indicators of site index will therefore be examined in some detail. In table 20 the percentage frequency is shown for each species (or genus) in each of the four classes into which the site-index distribution is divided. The frequencies are based on the total number of occurrences of the species in all site-index classes. They are grouped according to the species which had the highest frequencies in each of the four site-index classes so that the species most characteristic of each class are grouped together and arranged within the groups in alphabetical order.

Evidently individual species tend to be associated with certain ranges of site index more often than with others. There are a considerable number which are most frequently associated with the 51-60 and 61-70 site-index classes and relatively few in the two extreme classes. Those species which have the highest frequencies in a certain class usually have frequencies not much lower in one or both of the adjacent classes. The species which have 100 percent frequency in one class are almost all those of which there was only a single record. If additional occurrences had been noted they would doubtless have added representations in other classes. Even species which would be expected to be limited to an extreme and narrow range of habitat and therefore of site index, show considerable variation. For example, *Comptonia asplenifolia*, although it has a high frequency in the 30-50 class, occurs also in the two higher classes. On the contrary, *Acer saccharum,* a climax dominant which would be expected to indicate habitats of high productivity, is represented in all four of the classes, and has a low indicator value. On the whole, the conclusion seems justified that individual species do not characterize the site index of aspen specifically enough to be used for prediction with any degree of confidence, even within a range of as much as 10 site-index units.

The plant-indicator value of individual species is distinctly less than that of groups of species, on the same basis of classification. Furthermore, group-

TABLE 20. FREQUENCY PERCENTAGES FOR INDIVIDUAL SPECIES IN SITE-INDEX CLASSES

Species	Class 30-50	Class 51-60	Class 61-70	Class 71-90
Poor site indicators:				
Chamaedaphne calyculata	100			
Chimaphila umbellata	50		50	
Comptonia asplenifolia	72	14	14	
Lycopodium complanatum	38	38	16	8
Populus grandidentata	50	25	13	12
Quercus ellipsoidalis	50	50		
Rubus parviflorus	50	.	50	
Fair site indicators:				
Abies balsamea	13	39	38	10
Acer rubrum	11	50	31	8
Amelanchier laevis	5	47	43	5
Aster macrophyllus	9	40	37	13
Betula papyrifera	11	41	36	12
Corylus rostrata	9	42	36	12
Cypripedium acaule		100		
Epigaea repens		67	22	11
Epilobium angustifolium		100		
Equisetum arvense		64	36	
Gaultheria procumbens	40	47	13	
Hepatica triloba		56	33	11
Impatiens pallida		100		
Larix laricina	25	33	33	9
Lathyrus ochroleucus and *L. venosus*	3	52	37	6
Ledum groenlandicum		100		
Linnaea borealis	11	56		33
Maianthemum canadense	6	37	33	24
Mitella nuda		54	23	23
Nemopanthus mucronata		100		
Osmunda claytoniana		100		
Picea canadensis	14	40	37	9
P. mariana	18	45	32	5
Pinus banksiana	16	54	30	
P. resinosa	21	53	26	
P. strobus	21	42	28	9
Polygonatum biflorum		52	48	
Prunus pennsylvanica	31	35	34	
P. serotina	25	25	25	25
Pteris aquilina	10	41	38	11
Quercus borealis	19	50	19	12
Ribes cynosbati	4	41	33	22
Rubus (argutus?)	17	68	17	
R. strigosus		50	40	10
Salix sp	20	41	36	3
Solidago sp.		80	20	
Sphagnum sp.		44	33	22
Streptopus longipes		50	42	8
Taxus canadensis		100		
Vaccinium canadense	18	68	14	.
Good site indicators:				
Acer saccharum	8	36	43	13
A. spicatum	2	33	40	24
Actaea		40	40	20
Alnus incana	2	33	52	13
Amphicarpa monoica			100	
Apocynum androsoemifolium		14	43	43
Aralia nudicaulis	5	38	44	13
Asarum canadense		37	37	26
Asplenium filix-femina	3	23	49	26
Betula lutea			84	16
Clintonia borealis		39	45	16
Coptis trifolia	21	29	50	
Cornus canadensis	11	39	44	6
C. (not *canadensis*)		39	43	18
Cypripedium parviflorum			100	
Diervilla lonicera	11	33	45	10
Fragaria virginiana	7	37	42	13
Fraxinus nigra		44	56	
F. pennsylvanica var. *lanceolata*		19	55	26

TABLE 20. *(Continued)*

Species	Class 30-50	Class 51-60	Class 61-70	Class 71-90
Galium triflorum		36	45	19
Geum virginianum			50	50
Gramineae	10	33	51	6
Iris versicolor			100	
Lonicera canadensis	5	33	52	10
Lycopodium obscurum var. *dendroideum*	3	41	47	9
Mitchella repens	.		100	
Ostrya virginiana		12	75	13
Petasites palmatus	.	38	46	15
Populus balsamifera		42	50	8
Prunus americana			86	14
P. virginiana		37	47	16
Pyrola spp.	8	25	58	9
Quercus macrocarpa		22	52	26
Rhus toxicodendron		38	54	8
Rosa sp.	3	15	61	21
Rubus pubescens		24	52	24
Smilacina racemosa		26	63	11
Sorbus americana		38	62	
Thalictrum dioicum	3	23	52	22
Thuja occidentalis	13	33	47	7
Tilia americana		17	57	26
Trientalis americana		35	48	17
Tsuga canadensis		25	50	25
Ulmus americana	.	7	61	32
Uvularia grandiflora		29	47	24
Viburnum spp.		37	37	25
Viola spp.	..	11	78	11
Excellent site indicators:				
Carex spp.	..	20	.	80
Carpinus caroliniana	..	..	.	100
Dirca palustris	..	..	50	50
Onoclea sensibilis	..	.	.	100
Trillium grandiflorum	..	20	40	40

ings of species according to site-index or soil classifications are less satisfactory than one in which species are grouped according to their associations in natural communities. This is particularly true if the groups are used to establish the relations with both habitat and growth or with more than the one set of factors on which the plant-indicator classification is based.

SUMMARY AND CONCLUSIONS

The records from 277 sample areas of the aspen community in northern Minnesota and northwestern Wisconsin, a region of relatively uniform climate, have afforded the opportunity to evaluate quantitatively the interrelations between habitats, plant indicators, and the growth rate of aspen.

The habitat classifications, according to soil texture, surface geological formation, a combination of texture and surface formation, and soil type and profile groups, represent a series which comprise successively larger proportions of the total number of edaphic factors which influence the floristic composition and growth of plant communities. Texture classes reflect chiefly the aeration and moisture relations in the surface 8 inches. Surface formations express also the aeration and moisture relations, less definitely for the surface but more adequately for the subsoil, and, in addition, the ground water and drainage factors. The combination of texture class and surface formation integrates the factors of the two separate bases for classification.

Soil types and profile groups synthesize all of the factors, physical, chemical, and biological, which influence plants as they do the processes of soil formation.

As a measure of the degree to which each of these classifications corresponds to the growth of the aspen community, the correlation ratios between soil groups and mean site index of the aspen plots of each group, gave the following results:

Basis of classification	*Correlation ratio*
Soil-texture class	0.573
Surface formations	.640
Soil-texture classes and surface formations	.699
Soil-profile groups (12)	.788

The correlations become successively closer as the soil classifications represent larger proportions of the growth factors of the habitats. The soil profiles offer the best foundation for the differentiation and prediction of the productivity of the different habitats for the growth of aspen.

Site index, a measure of the height growth of dominant aspen, is a better criterion of habitat productivity than is volume growth. This is indicated by the correlation ratio of 0.699 between site index and of 0.461 between volume index and the soil texture-surface formation groups. This superiority obtains notwithstanding the fact that the correlations were based on all the plots for site index and on only the well-stocked plots for volume index, thus in the latter case minimizing the influence of density, one of the important sources of variation in growth rate.

The associations of plants of the aspen community with other natural communities, as determined by the maximum frequency for each plant in the different communities, affords another and independent basis for the classification of the habitats. Classified in this way, the natural community groups have a correlation ratio with the mean site index of aspen of 0.761, superior to any of the soil groupings except the 0.788 with the soil-profile groups. Thus natural community plant-indicator groups rank very close to the soil-profile groups for the prediction of the productivity of the habitats for the growth of aspen.

Tests of the significance of the differences in mean site index of aspen between the categories of the texture-surface formation, soil-profile, and natural community classifications indicate that in each case only about four combinations of groups are distinguishable, as judged by the variability of the site-index values. The fact that this same limitation is derived from three independent sources suggests that, as the number of subdivisions of any habitat classification is increased, a point is reached at which the local and individual variations of soil and vegetation within the categories become as great as the differences between categories. As measured by the growth of

aspen, this point is reached when the combined groupings are so few and broad that they have little physical and biological homogeneity. In several intances they comprise groups of very diverse characteristics except with respect to the growth of aspen. The conclusions may be drawn, first, that the habitats of the aspen community in the region represent about four distinguishable site qualities for the growth of aspen; and, second, that physical or biological classifications of the aspen habitats do not always differentiate productivity classes or site qualities, all of which are distinct in respect to the growth of aspen.

The 54 soil types represent more nearly homogeneous unit habitats than any of the broader categories of classification. At the same time, many of them are not distinguishable as measured by the growth of aspen or by the plant indicators. Their homogeneity is obscured when they are combined into larger groups which have biometrically significant differences. Because this process is necessary in order to use the soil types in relation to the growth of aspen, their value for the purpose is relatively small.

Habitat groups based on edaphic characteristics are not specifically differentiated by individual plant indicators. Only a few of the low frequency species have specific indicator value for individual habitat groups and their infrequent occurrence seriously detracts from their usefulness. The abundant and high frequency species are nearly ubiquitous in the aspen community and therefore have little or no indicator value. The relation between soil groups and individual plant indicators is not sufficiently close to enable the satisfactory prediction of one by means of the other.

If the plant indicators are combined in 16 natural community groups and thereby are related to the 22 soil-profile groups, a certain degree of correlation is obtained, although it cannot be satisfactorily expressed biometrically with the relatively few data available. If these groups are condensed to six in each category, forming as nearly as possible homogeneous classes, a coefficient of contingency of 0.62 is obtained, indicating a significant and, considering the negative findings for the individual plant indicators, a surprisingly close association between the two series.

This association between plant indicator and soil-profile groups may be interpreted by the statement that, as the soils may be considered to form a progressive series from the immature, less well-developed, and less favorable groups to the mature, well-developed, and more favorable groups, so also the vegetation groups, by analogous steps, progress from the early successional stages, both xeric and hydric, to the hydro-mesic subclimax and mesic climax groups. In other words, the stages of the vegetational succession tend to be associated with a corresponding series as represented by the genetic development of the soil profiles.

The site index or growth rate of aspen is not characterized within a sufficiently narrow range for useful predictions by the individual species of the

associated vegetation of the community. Certain infrequent species seem to be relatively specific but have little value because of their uncommon occurrence. Almost all of the high-frequency species are associated with more than half of the total range of site index and therefore have little indicator value. Groups of species which are more representative of certain site-index classes than of others are readily segregated by their frequencies, and in the aggregate these groups have some value as indicators of aspen growth, just as the natural community groups were shown to have a relatively close correlation ($\eta = 0.761$) with site index.

The more important of the foregoing conclusions may be epitomized and brought into relief in a final paragraph. Site index of aspen is a more reliable measure than volume growth, and may be used satisfactorily for the evaluation of the differences and relative productivity of the aspen habitats. Conversely, the habitat groups, which may be established most effectively on the basis of soil profiles, may be used within limits for the prediction of the average growth of aspen. Individual plants of the aspen community do not indicate with sufficient reliability differences either in the habitats or growth rates of aspen. Groups of plant indicators, of which the most satisfactory are those based on maximum frequencies in natural communities other than aspen, together with the soil-profile groups, are the two most useful classifications for the differentiation and for the prediction of the productivity of the different aspen habitats.

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TERMITE NESTS—A STUDY OF THE PHYLOGENY OF BEHAVIOR

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TERMITE NESTS—A STUDY OF THE PHYLOGENY OF BEHAVIOR

INTRODUCTION

Almost every naturalist who travels in tropical countries observes the striking nests of termites and many figures of these nests have been published (Hegh 1922). The significance of termite nests to biological theory, however, has been only partially stressed, although Darwin (1859) places considerable emphasis upon the evolution of "instinct" as illustrated by "neuter and sterile insects." He states:

> But I must confess, that, with all my faith in natural selection, I should never have anticipated that this principle could have been efficient in so high a degree, had not the case of these neuter insects led me to this conclusion. I have, therefore, discussed this case, at some little but wholly insufficient length, in order to show the power of natural selection, and like-wise because this is by far the most serious special difficulty which my theory has encountered. The case, also, is very interesting, as it proves that with animals, as with plants, any amount of modification may be effected by the accumulation of numerous, slight, spontaneous variations, which are in any way profitable, without exercise or habit having been brought into play. For peculiar habits confined to the workers or sterile females, however long they might be followed, could not possibly affect the males and fertile females, which alone leave descendants. I am surprised that no one has hitherto advanced this demonstrative case of neuter insects, against the well-known doctrine of inherited habit, as advanced by Lamarck.

Subsequent writers have referred to Darwin's statement and have used the sterile castes as an argument against the Lamarckian concept (Ball, 1890, 1894; Weismann 1893; Holmes 1911), but the rich recent information made available through greater exploration and systematic study of tropical faunas has not yet been adequately interpreted. I propose, in the following pages, to present the best cases known to me illustrating the principles of evolution as applied to termite nesting behavior.

I am indebted to Mr. G. F. Hill, Senior Entomologist in the Division of Economic Entomology in Australia, an eminent contributor to our knowledge of termites, for the photographs of Australian termite nests. The African nests were photographed by Mr. Herbert Lang while on the Lang-Chapin expedition of the American Museum of Natural History during which he made a splendid collection of termites and took many valuable field notes. The other photographs were taken by the author or under the author's direction.

Studies of north African and European termites were made by the author during the tenure of a John Simon Guggenheim fellowship, during which time Dr. F. Santschi and Dr. F. Silvestri were particularly helpful. Studies

in British Guiana were made at the Tropical Research Station of the New York Zoological Society at Kartabo, and I am greatly indebted to the director, Dr. William Beebe, for the opportunities he afforded. Studies in Panama were largely made at the Barro Colorado Island Laboratory of the Institute for Research in Tropical America. The author is indebted to Mr. James Zetek for many courtesies extended during his sojourn on the island. My thanks are due Mr. George Lee for the opportunity to study savannah termites in Panama. For the opportunity to study Californian termites, I am indebted to the Termite Investigations Committee and particularly to Dr. C. A. Kofoid and Dr. S. F. Light.

I am also grateful to many men interested in this problem with whom I have had conversations or correspondence, although they should not be held responsible for any erroneous views expressed in the following pages. Among them all, I should particularly mention Dr. W. C. Allee, Mr. G. F. Hill, Dr. N. A. Kemner, Dr. H. Klüver, Dr. T. E. Snyder, Dr. W. M. Wheeler and Dr. Sewall Wright.

TERMITE NESTS AS ILLUSTRATIONS OF BEHAVIOR EVOLUTION

The nests of termites have certain attributes which make them objects of great biological interest. These may be listed as follows:

(1) The nest structures are morphological expressions of behavior patterns. This quality makes aspects of behavior evolution as visible as morphological evolution and similar principles and terms may be directly applied.

(2) The nest results from the activity of a large number of individuals cooperating in building, organizing and enlarging the structure. Individual variation is thus practically cancelled and the nest stands as an expression of the behavior of a population.

(3) The nest-forming behavior is predominantly an inherited species-pattern. The nests of a given species show striking similarity in material, general shape, internal organization and ecological position. In most instances, the workers which construct the nest have had no contact with workers of other colonies. The reproductive castes, which do not exhibit complicated nest-building behavior, fly from the parental nest, pair, and lay eggs which develop into workers which again establish a nest with the specific characteristics of the parental nest.

(4) The caste which builds the nest in all the higher termites is the sterile worker helped, in some cases at least, by the larger soldier nymphs. Thus we have a complete control over any possibility of the inheritance of an acquired character. No nest-building habit or structural modification of a sterile caste acquired during ontogeny could be transmitted to the succeeding generation. This control over any Lamarckian influence is even better than that found in other social insects. Workers of wasps, bees and ants, although without

socially functional young in most cases, not infrequently lay eggs which, being unfertilized and haploid, develop into fertile males. This is not known among termites. Workers of termites may, therefore, be considered as somatic individuals, physiologically separated from the germ plasm of the reproductive individuals, making a directive influence upon the genetic determiners a practical impossibility.

(5) The nests are definitive enough and at the same time specific enough to give us excellent evolutionary sequences. These may be correlated with the known morphological evolutionary relationships of the species. We have nest sequences of species in the same genus available, information that should give us a clue to the influence of species divergence upon these behavior patterns. In numerous instances we also find nest characteristics common to many species within a single genus or a group of related genera, thus indicating a long stability of the inherited patterns.

(6) Astonishing examples of adaptive modification of the nests together with convergent evolution of nest structure in certain environments present evidence of the force of selection acting upon the inherited patterns.

(7) The evolution of the nesting behavior is one aspect of the evolution of polymorphism. The colony of polymorphic insects has many attributes of the individual multicellular organism and exhibits many interesting parallels to organismal coordination mechanisms and interrelations of parts. Natural selection probably acts upon the colony as a whole more than upon the individual termite.

PRE-ISOPTERAN NESTING BEHAVIOR

The available indications point toward excavation of wood as the primitive nesting behavior. Certain wood-eating roaches, such as *Cryptocercus punctulatus* Scudder, probably represent the closest approach to the activities of the blattoid ancestors of the termites. Cleveland (1934, p. 190) describes the excavations of this roach as follows:

> The wood is honeycombed with galleries which, for the most part, run parallel with the grain. In some of the sounder logs, particularly chestnut, which is often very hard, the roaches are seldom found near the outside. * * There is little evidence that they ever leave the log and enter the ground. * * They pass well-formed pellets of dry, woody material which is not utilized in any way for building purposes or for the construction of passage ways, differing in this respect from many species of more highly specialized termites.

With reference to excavations for the ootheca, Cleveland (p. 207) states:

> a groove had been made in the wood where none existed before and the ootheca had been carried approximately six inches, placed in the groove, and sealed off so completely that only a portion of one end was visible.

These observations and others indicate the probability that habitations in excavated wood and the care of the eggs, as well as wood-feeding, symbiotic relationship with gut-inhabiting protozoans, and development of a family organization, antedated the origin of the Isoptera.

NESTING BEHAVIOR OF THE KALOTERMITIDAE

Among the living termites, *Mastotermes darwiniensis* Froggatt (Mastotermitidae) is universally admitted to be the most primitive morphologically. However, the descriptions of its nesting activities (Hill 1921, 1925) would seem to indicate an advance over the behavior of kalotermitids usually considered more advanced from a morphological standpoint. As Imms (1919) and Emerson (1926, p. 92) have remarked, in certain morphological details *Archotermopsis* (Kalotermitidae) is more primitive than *Mastotermes*. One may either conclude that *Mastotermes* has undergone evolution toward more intricate behavior after its divergence from the ancestral isopteran stock, or else that degenerative evolution of the behavior patterns has occurred in the Termopsinae and other kalotermitids. With only meager evidence, I am inclined toward the former hypothesis.

From morphological considerations, *Archotermopsis wroughtoni* (Desneux) is the most primitive living member of the Kalotermitidae. The following description of the nest is taken from Imms (1919, p. 126), who also figures the galleries:

> Any structure which might be designated a termitarium or nest is absent, and the bulk of the members of a colony are to be found in irregular chambers situated in the decayed portions of a tree trunk. The wood is perforated in various directions by large galleries or tunnels. Certain of these passages pass outwards in a radial direction terminating just beneath the bark, if the latter be present. The majority, however, run in a longitudinal direction following the grain of the wood. The insect does not construct tunnels of cemented material on the surface of the tree trunk or the ground, as is the custom among a very large number of Termites. There is usually, therefore, no outward manifestation of its presence, which probably accounts for the insect having so long remained a rarity. When necessary, however, it closes up crevices by means of a cement of masticated ligneous material, or of excrementous matter held together by salivary secretion. The centre of a colony is occupied by the ova and very young larvae, and in their immediate vicinity the queens and kings are to be found.

The above description also applies to the nests of species in the related genus, *Zootermopsis*, found in the western United States. These species have been classed by Light (1934, v. 136) as "damp-wood termites" because they seem to be more dependent upon moisture than the majority of the Kalotermitidae which are often classed as "dry-wood termites." Both the damp-wood and dry-wood termites may live wholly within excavated wood and usually do not invade the soil, although in certain instances, notably *Kalotermes (Paraneotermes) simplicicornis* Banks, soil excavations may be found (Light 1934, p. 140; 1937).

EXCAVATING BEHAVIOR OF THE KALOTERMITIDAE

Although the excavation of wood is probably the most primitive behavior for the construction of a protected nesting site, the responses to environmental factors are quite intricate. A cork in a test-tube containing a captive colony of *Kalotermes flavicollis* (Fabricius) was invaded by the termites through small openings about the diameter of the larger nymphs. The end of the cork was cut off with a knife and revealed the excavations of the termites (Fig. 1). Through examination of the figure, it will be noted, in the first place, that the galleries are elongated and are strikingly correlated with the spring growth rings, only occasional passageways being found in the summer growth rings. This is probably a reaction to mechanical stimuli, although these rings doubtless differ in chemical composition as well. Secondly, it will be noted that the termites excavate close to the surface, but do not penetrate the surface. The layer between the excavation and the outside is so thin that light shines through when the cork is held up to the light.

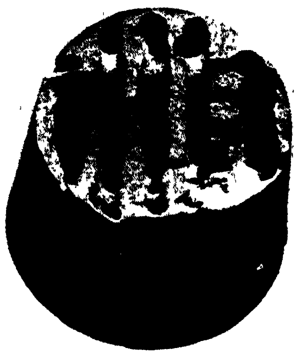

FIG. 1. Cork excavated by *Kalotermes flavicollis*

One might classify this phenomenon as a reaction to light, to changes of humidity or to a weakness in the thinner layers of cork. If pieces of wood within a test tube are subject to the attack of termites, no such thin layer is left, thus indicating that the weakened material is not the only factor, although the termites would seem to be sensitive to such differences. Likewise, termites do not avoid light shining through glass test tubes or containers, providing the light is not too hot and the humidity is not lowered materially. Toleration experiments and experiments with a humidity gradient conducted by Williams (1934) indicate sensitivity to humidity in most cases studied, although some of the Kalotermitidae do not seem to be highly sensitive to low humidities. Pending further experimentation, it would seem to me that a change in humidity was the factor dominantly responsible for the separation of the excavations from the exterior. Pillars of corky material are to be seen in the photograph. These have been left around the hollow lenticel pores in the cork running at right angles to the growth rings. Such pillars are probably best interpreted as reactions to changes in humidity.

To what extent the excavating termites respond to stresses and strains in the wood has not yet been satisfactorily determined, although the problem is open to experimental attack. Observations, particularly by those investigating damage to building construction wrought by termites, seem to indicate

that termites will not weaken timbers sustaining weights to the point of collapse. If such timbers collapse, extra strains have been placed upon them through storms, earthquakes, or additional weights to which the termites have had no opportunity to react while making their excavations. Spatial factors may also play a rôle but have not been much investigated.

There is little to indicate that the presence of the king, queen, young or eggs influence the excavation activities of the Kalotermitidae. These primitive termites do not have grossly enlarged queens and the reproductive castes are usually found in galleries approximating the size and general appearance of the other galleries. Eggs may be found in the cells occupied by or near the reproductive castes. They may be picked up and gathered into small groups by the nymphs as has been observed by the author in captive colonies of *Zootermoposis angusticollis* (Hagen) and *Kalotermes flavicollis*.

CONSTRUCTION BEHAVIOR OF THE KALOTERMITIDAE

Although excavation as the result of feeding activities supplies termites with a protected nesting site, positive constructions supplement the burrows in producing habitations even in the most primitive kalotermitids.

After the colonizing flight and subsequent pairing, the reproductive couple of *Kalotermes minor* Hagen excavates a small hole or cell in available wood and plugs the entrance. Harvey (1934, p. 225) states: "This plug is a mixture of partially chewed wood and a secretion of the termites which acts as a cement."

The worker-like nymphs of a mature colony of *Zootermopsis angusticollis* kept in a quart mason jar built extensive partitions separating cells in the excavated wood and also connecting the wood with the glass. These partitions were made largely from the pellets of excrement which were cemented by saliva, and by liquid excrement which was extruded upon the pellets worked into place by the mouth-parts. Small experimental holes made in the metal cover of the jar were plugged in a similar manner. The nymphs would seem to react directly to changes in humidity, although other factors may also contribute to the cooperative action involved in building a partition.

Such building activities as those described for *Kalotermes* and *Zootermopsis* are probably to be found with little variation throughout the Kalotermitidae. In a few instances, permanent runways may be excavated through soil which enable the termite colony to exploit food resources outside the nest. Such runways are not common in the Kalotermitidae, but have been reported by Light (1934a, p. 311; 1937).

NESTING BEHAVIOR OF THE MASTOTERMITIDAE AND HODOTERMITIDAE

Hill's (1921, 1925) accounts of the nests of *Mastotermes darwiniensis* leave little doubt that the nesting behavior must be more specialized than

that found in the Kalotermitidae. The nests are subterranean and are not always closely associated with the feeding excavations. Extensive construction and covered galleries are reported; the colonies contain over a million individuals, and foraging termites may destroy wooden materials over a hundred yards from the nest.

Even though this account gives the impression of rather specialized nesting behavior, it would seem to differ quantitatively rather than qualitatively from that of the Kalotermitidae.

The hodotermitids seem to be an offshoot of primitive kalotermitids or possibly pre-kalotermitids. Their social organization indicates considerable specialization beyond that observed in the Kalotermitidae. They have become harvesters and feed largely upon grass; they have an active, pigmented caste with compound eyes which forages on the surface in the day time and is usually considered an adult worker, a caste which seems to be lacking in the Mastotermitidae and Kalotermitidae.

Accompanying the evolution of structure and social integration, we find elaborate nesting behavior transcending anything observed among other primitive termites. Fuller (1915) has given excellent descriptions and figures of the nests of the South African species of this family (also Hegh 1922, pp. 232, 233). The nests of *Hodotermes (H.) mossambicus transvaalensis* Fuller are built in excavated chambers under the surface of the earth. The soil is brought to the surface and dropped in small piles which are distributed by the rain. Fuller (p. 350) states:

> The hive-cavities, with one exception, were all sub-spherical, having a horizontal diameter of 24 in. and a perpendicular height of 18 in. The cavities are partitioned by very numerous horizontal and close-set shelves. These are constructed of a thin and very papery substance which does not dissolve in water or in alcohol. The shelves lie one above another with striking regularity, and are attached to a series of clay brackets projecting from the walls. The shelves are not equi-distant apart throughout the cavity, but range from 6 to 15 mm. Innumerable little cylindrical columns of wooden texture, spread over the field of each shelf, hold the whole fabric together. These little columns are not stairways; the insects pass up and down from storey to storey of the hive by short inclines.

Of particular interest is the construction of the supporting columns. It would seem necessary to assume an intricate reaction to strains in the nest material to account for such elaborate architecture.

Nests of *Hodotermes (Anacanthotermes) ochraceus* (Burmeister) which I examined on the outskirts of Kairouan, Tunisia, consisted of soil excavations without surface indications except that the soil particles had been cemented together over the cells near the surface forming a brittle cover which gave off a hollow sound when lightly tapped. Some of these cells were filled with strips of plant epidermis from the stems of surrounding scrub vegetation. A tiny termitid, *Eremotermes indicatus* Silvestri, was

found living in these storage cells feeding upon the food gathered by *H. ochraceus*. Extensive chambers contained all stages of nymphs and all castes of *H. ochraceus*.

A mason jar was filled with soldiers and various sizes of "workers." The smallest was about ½ cm. long and the largest about 1 cm. long. Soil together with strips of plant epidermis collected by the termites was also included. The termites immediately started to construct passageways and galleries and to accumulate the food. The construction was performed by working pieces of dirt moistened by saliva into place with the mouth-parts. No abdominal excretion was observed during the construction activities. All sizes of "workers" including the next to the smallest engaged in the labor.

These data indicate a much more developed nesting behavior in the Hodotermitidae than has been found among the Kalotermitidae. The emancipation from a wood diet, the construction of subterranean galleries, the storage of food, and the subtle manipulation of materials in the construction of complex layers of cells, passageways and supports; all indicate greater elaboration of the inherited behavior patterns than is found elsewhere below the Termitidae.

NESTING BEHAVIOR OF THE RHINOTERMITIDAE

The family Rhinotermitidae was derived, according to the available morphological evidence (Hare, 1937), from a kalotermitid stock fairly closely related to *Stolotermes*. The social development is much more marked than in the Kalotermitidae and a true sterile adult worker caste has become differentiated. Specialization of the worker is accompanied by larger numbers of individuals in the colonies, enlargement in size and reproductive capacity of the queen, incorporation of certain specialized termitophiles into the social community—all indicative of more complex social organization.

Excavations and passageways in the soil enable these insects to reach soil moisture which seems to be necessary for their existence in nature and also enables them to exploit food resources remote from their nests. Because of their adjustment to soil conditions, they are typical "subterranean termites" and have been so classed by Snyder (1920, p. 89).

The development of more elaborate nesting behavior might be expected in this family, but in reality the nests are still largely to be found in excavated galleries in wood with somewhat more complex cells, partitions and covered tunnels than are characteristic of the Kalotermitidae.

The more elaborate nest structures among the Rhinotermitidae are made by certain species of *Coptotermes*. Oshima (1919) has published some excellent figures of the nests of *C. formosanus* Shiraki. He states (p. 333):

> The nest consists of a mixture of abdominal excreta and clay or sand, pasted together with a special secretion of the salivary glands. Sometimes

it is rigid and compact and seems like a piece of rock. However, it is inflammable and burns rapidly, leaving a small amount of ash.

Ehrhorn (1934, p. 327, 329) shows photographs of the nests of the same species and Light (1934, p. 142) figures the nests of *C. vastator* Light. Hill (1915, p. 92) gives an excellent description of the nests of *C. acinaciformis* (Froggatt) accompanied by photographs. This species builds conspicuous mounds usually found at the base of a tree or enveloping a stump. The mounds may reach a height of six to eight feet. The walls of these nests are constructed of fine particles of earth and sand firmly cemented together. The walls vary in thickness from two inches near the top to twelve inches near the ground or on the sides. The interior is composed of triturated wood molded into curious forms. Near the ground are found thin-walled horizontal cells serving as the "nursery." Hill also states:

> The queen is generally found about three inches from the ground, and about the middle of the nest, in a low domed cell with more or less level floor, from which she cannot excape.

It is apparent that the nests of *Coptotermes* illustrate the use of various materials, the organization around social functions, and reaction to the presence of the queen resulting in the construction of a "royal cell."

During the colonizing period it is necessary that exits from the nest be made in order to allow the imagoes to emerge. Holes are excavated by the workers in all cases observed and the soldiers guard the exits during the emergence of the imagoes. The exits are plugged by the workers at the end of the flight. Two instances of building activity associated with the colonizing flight have been observed. Wood of a beam in a small house three miles from Kartabo, British Guiana, was infested with *Coptotermes testaceus* (L.). On the morning of July 2, 1924, Dr. S. C. Crawford and the writer noticed workers constructing a small shelf about an inch long, a half inch wide and a half inch high, at the mouth of a small excavated hole in the wood on the vertical face of the beam. Soldiers guarded the operations. About two hours later a light rain fell and as it ceased, flying imagoes of the species were noticed. They were soon discovered emerging from the hole in the beam and using the shelf as a platform from which they took to the air. The next morning only a plugged hole was visible, the workers having dismantled the shelf during the night. Mr. James Zetek observed a somewhat similar construction during a flight of *C. niger* Snyder from the base of a tree in Ancon, Canal Zone, on August 26, 1923.

It is extremely difficult to analyze such behavior in terms of responses to simple stimuli. Although our ignorance is great, one must assume responses to intricate social stimuli. Anthropomorphic explanations, however, do not assist our understanding.

NESTING BEHAVIOR OF THE TERMITIDAE

The Termitidae are morphologically and socially the most specialized of the termites and have doubtless evolved from a rhinotermitid stock. The abundance of nest types are too numerous to describe in this report and only a few of the more outstanding and significant examples will be mentioned.

Many nests of the Termitidae are not more elaborate than the simplest nests of the Rhinotermitidae. In fact, some nests seem even less complex. The author dug into a subterranean nest of *Syntermes snyderi* Emerson in the rain-forest of British Guiana (Fig. 2) and found galleries extending

FIG. 2. Subterranean excavated nest of *Syntermes snyderi.*

below the surface to a depth of about four feet and covering a horizontal circular area with a diameter of about twelve feet. The galleries were large and seemed to be simple excavations in the sandy-clay soil, although there were small lumps lining the galleries in places that might have been excretions of the termites. The excavated dirt was deposited on the surface in

loose piles above the nest. No covered tunnels were constructed on the surface, the termites moving in exposed trails. They cut out pieces of dead leaves which served as their food. Leaf fragments about one centimeter in diameter were stored in some compartments of the nest.

The humidity and consistency of the material composing the walls of the excavated galleries must be fairly constant in such a nest. The excavating termites would seem to be reacting to spatial factors as well as to strains in the supporting walls, rather than to humidity or differentiation of material as in the case of *Kalotermes flavicollis* described in the preceding pages.

NEST MATERIALS

Materials composing the nests of termitids (see Hegh, 1922) are similar to those already described, but one often finds a given group specializing in the use of certain substances. Most of the species use particles of dirt or sand. The nest of *Anoplotermes (A.) silvestrii* Emerson in British Guiana was of such extreme hardness that sparks flew from the hatchet when the nest was opened. In laboratory colonies, no abdominal excretion was observed during the nest building activities. Each particle of dirt was moistened only with a salivary secretion as the worker placed it in position. Laboratory colonies of *Microcerotermes arboreus* Emerson, however, revealed the workers·placing pieces of dirt moistened with saliva in place and then turning and excreting a drop of thick dark fluid upon the newly inserted particle. *Crepititermes verruculosus* Emerson exhibited still different actions. Practically all the building observed in the laboratory was constructed through the use of abdominal excretions of thick dark fluid. The intestines of the workers seemed to be filled with this muddy material. They were sometimes observed to bring pieces of material for building, but no salivary secretion was seen nor did they work the material into place in the manner so characteristic of most termites.

On the other hand, wood derivatives are used almost exclusively by the majority of the species of *Nasutitermes, s. str.* (Fig. 3), a tropicopolitan group of termites composed of a large number of species. These termites can build typical nests in such places as the branches of standing dead trees which have been killed by the rise of dammed waters in Gatun Lake during the construction of the Panama Canal. Such nesting sites are not available for species dependent upon dirt in the construction of their nests.

Beaumont (Dudley, 1889, p. 91) described the construction activity of a species of Panamanian termite (either *N. corniger* (Motschulsky) or *N. ephratae* (Holmgren). The behavior is essentially similar to that described for *Microcerotermes arboreus* except that particles of wood or carton are used instead of dirt. Bugnion (1927, p. 18) also gives a fine detailed account of similar behavior of *Nasutitermes (= Eutermes) ceylonicus* (Holmgren) which uses both wood, sand and abdominal excretions in its construction. An

interesting variation was observed by the author while watching captive colonies of *Nasutitermes guayanae* (Holmgren) in British Guiana. Instead of placing the piece of material in its position with saliva and then excreting

FIG. 3. New cells in process of construction during the enlargement of the nest of *Nasutitermes guayanae*.

abdominal fluid, the termite invariably excreted the abdominal substance first, and then turned and worked the piece of building material into place with it's mandibles.

STRUCTURES

The structures vary considerably in form and function (see Hegh, 1922), thus indicating a wide variety of stimuli affecting the behavior pattern. Covered tunnels may lead out from the nest. These are built along odor trails followed by the termites at times of high humidity. One of these covered tunnels built by *N. guayanae* led from a nest thirty feet up in a palm tree, down some vine stems to the ground, and around by a sandy clearing in the

forest to a small dead tree. In all, the distance was 162 feet, although the dead tree was only 35 feet in a straight line from the palm tree.

The covered tunnels may lead down into the ground where the excavations are lined with carton (materials cemented by saliva or excrement). Covered tunnels on the walls of Chilibrillo Cave, Panama, made by *N. corniger*, were estimated to be about twenty feet below the surface of the ground.

William Beebe observed *Macrotermes carbonarius* (Hagan) at Penang, Malaya, walking in open trails on carton roadways which the termites constructed over rough ground (See Emerson, 1937a, p. 247). I assume these roads to be a response to mechanical factors.

Termites will use the same materials used in the construction of their nest or tunnels for burying foreign insects introduced into their colony. Dudley (1889) has figured this action in *Nasutitermes* and the author has witnessed it many times following the attack upon an introduced foreign termite or termitophile.

The size of the nest is quite often fairly characteristic of the species. For example the nests of *N. pilifrons* (Holmgren) were quite often much larger than those of *N. corniger* or *N. ephratae* in Panama. Likewise in British Guiana, the nests of *N. surinamensis* (Holmgren) were typically larger than those of *N. guayanae*, *N. costalis*, or *N. ephratae* and, in turn, these were larger than the nests of *N. gaigei* Emerson. The huge dirt nests of *N. pyriformis* (Froggatt) reaching a height of 18 feet would seem to be characteristic of the species (Froggatt, 1905). The size of the nest may be proportional to colony size and reproductive capacity. The number of individuals in one nest (Emerson, 1937a, p. 247) of *N. surinamensis* was estimated quite carefully to be three million in round numbers. The nest measured six feet in height and three and one-half in greatest diameter. The queen from this nest was 24 mm. long and 8 mm. wide. She laid 2938 eggs in 18 hours. A small nest of *Microcerotermes arboreus* in British Guiana seemed small enough to count the entire colony (excepting foragers). It measured 6 in. long, 2 in. wide and 2 in. thick. The volume was approximately 110 cu. cm. There were 5876 termites and 2109 eggs in the nest. 4006 of the termites were mature and 1870 were nymphs. The mature individuals were composed of 1 queen, 1 king, 114 soldiers, and 3890 workers divided into 2624 large light-headed types, 939 small dark-headed types and 327 intermediates. Two larger nests of this same species contained about 250,000 eggs and 300,000 eggs respectively. A queen measuring 21 mm. in length laid 1680 eggs in 24 hours. The highest rate of oviposition which I have measured was 357 eggs in one hour in the case of a queen of *Anoplotermes silvestrii* which measured 50 mm. in length. These tropical queens continue to lay eggs steadily without much variation during diurnal or seasonal cycles and are doubtless often quite old. Through consideration of nests in Africa known to be at least

40 or 50 years old and each occupied by a first form queen, I think such an age for some of the reproductive castes is not impossible.

Enlargement of the nest may indicate some of the stimuli to which the workers respond. In the case of *Nasutitermes guayanae* (Fig. 3) a hole in

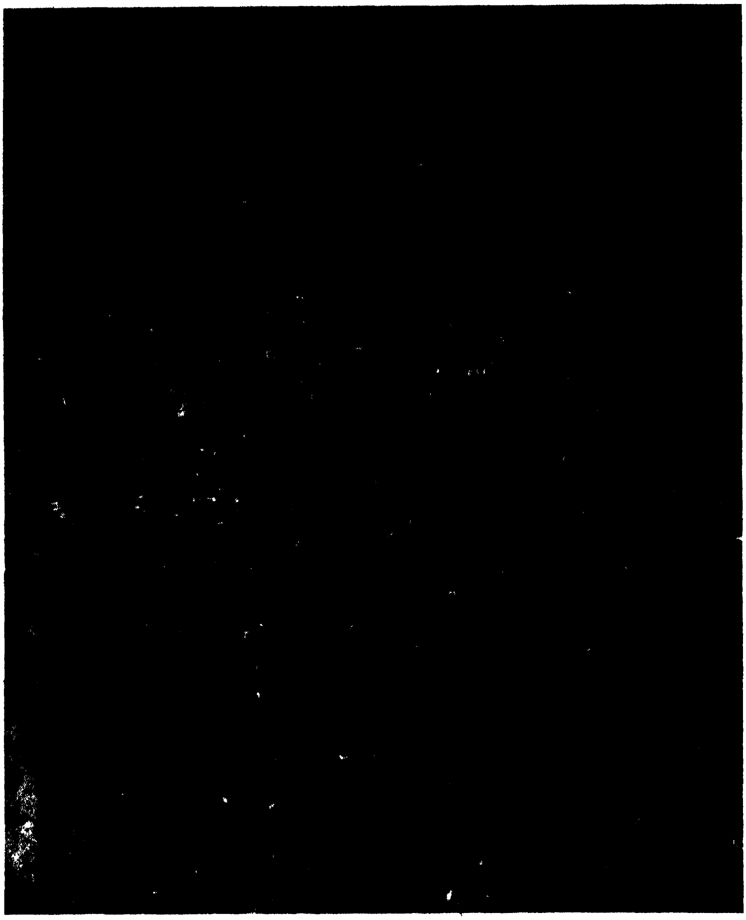

FIG. 4. Vertical section of a nest of *Nasutitermes costalis* showing the thick walls in the vicinity of the royal cell.

the exterior of the nest is made and a new cell is built over the opening. Workers build the walls on all sides until they meet at the top. *Constrictotermes cavifrons* (Holmgren) enlarges its nest by roofing the area between parallel surface ridges (Fig. 14). The point of junction between the walls is perfectly even and seems to be explained only in terms of subtle sensitivity to spatial relations. The subsequent thickening of the walls of the cells takes place below the surface. The walls in the vicinity of the royal cell are greatly thickened in the nests of many species of termites (Fig. 4) evidently stimu-

lated by the presence of the queen. Grassé (1937) gives an interesting and detailed account of the organization of the nest of *Macrotermes (Bellicositermes) natalensis* including consideration of the royal cell.

Holdaway (1933) gives interesting data upon the chemical differences in materials composing the parts of the mound nests of *Nasutitermes (= Eutermes) exitiosus* (Hill). An analysis of the inorganic material shows that the outer wall averages 64 per cent, the inner wall 15 per cent, and the "nursery" 11 per cent. There seems little doubt that social and environmental factors influence the use of materials in the same nest.

FIG. 5. Mound nest of *Amitermes medius* Banks. Aguadulce, Panama.

By far the most astounding structural detail in the construction of nest walls is to be found in the subterranean nests of the various species of the African genus *Apicotermes*. Careful descriptions and figures of these nests have been published (Desneux 1918; Hegh 1922, pp. 385-394, 712; Sjöstedt 1923, 1926, Taf. 13; Reichensperger 1923). The determination of the known species is to be found in Sjöstedt (1926, p. 153). The simplest of these nests has external walls perforated by tiny pores or channels too small for the termite to walk through and probably functioning as ventilation pores. The next most complex nest has the external openings of the pores emerging into small pits or holes considerably wider than the pores, and the most complex nests have circular galleries within the walls connected to the outside by small pores and to the inside by small pores of approximately equal diameter. In the latter case, it would seem difficult not to assume that the pits or holes of the second type of nest had evolved into the circular galleries of the third type. Such behavior evolution would seem to present a sequence which reminds one of the ascon, sycon and leucon types of canal systems in the sponges. The nests of *Apicotermes* also illustrate most clearly the inherent nature of the hereditary influences upon the behavior which are generic in character rather than distinctive of species alone. Of course we might expect to find certain types of behavior characteristic of larger groups than genera, and such is the case. The finest example of distinctive construction behavior characteristic of an entire subfamily (Macrotermitinae) is discussed later.

Kinsey (1936, pp. 8, 56, 57) reviews current concepts of higher taxonomic categories. Among others, the concept that genera, subfamilies and families are arbitrary groupings merely for the convenience of the taxonomist and

without objective reality has often been stated. The correlation of many morphological characteristics together with behavioristic, physiological, ecological and geographical characteristics as seen in the genera, subfamilies and families of termites has convinced the author that the groups of species are indicative of a relationship which may be scientifically symbolized in the names of the higher categories which thus rest upon sound objective evidence with statistical significance of correlation.

As has already been pointed out, food is sometimes stored in the cells of the nests of *Hodotermes* and *Syntermes*. Food storage may involve construction activity also. In the nest of *Constrictotermes cavifrons* (Fig. 14) the basal hanging portion is composed of a dark pasty material which I interpret to be stored food. It is possible, however, that this is segregated excrement. In any case, the material has sufficient nutrient value to be used by a large number of other insects including tineid caterpillars probably belonging to the genus *Amydria* or *Exoncotis* (det. W. T. Forbes), larvae of an acanthocerid of the genus *Acanthocerus*, elaterid larvae, larvae of the sciarid genus *Sciara*, and finally another species of termite, *Termes* (= *Mirotermes*) *inquilinus* (Emerson). *T. inquilinus* has never been found in any other place and I am confident that it is confined to the nests of *C. cavifrons*. Its galleries are separated from those of the host termite and are lined with carton of its own construction, but the nesting activities largely consist of excavations in the stored organic material deposited by the host termite. If the two species come together when the nest is opened, a violent battle ensues. Although the nests of the genus *Termes* are not as definitive as those of most species of *Nasutitermes*, it seems safe to assume that this particular species of *Termes* has undergone degenerative evolution of the nesting behavior in association with its social semi-parasitism. The closest related species, *Termes fur* (Silvestri), seems to have the same relationship to *Constrictotermes cyphergaster* (Silvestri) (Silvestri 1903, p. 128). These cases remind one of the evolutionary degeneration of the nesting behavior among the parasitic birds and the genus *Psithyrus* of the bumble bees.

Kemner (1929) interprets the existence of carton nodules in the nests of *Microcerotermes depokensis* Kemner as food storage activity. Similar nodules were observed in nests of *Nasutitermes pilifrons* during my studies of Panamanian termites, but I am not sure of their function.

Probably the most remarkable construction activities associated with nutrition are to be found in the fungus gardens of all species of the subfamily Macrotermitinae. The excrement of the termites or finely pulverized plant material (see Grassé, 1937) is built into elaborate convoluted structures so organized as to give a maximum surface for the growth of the fungus (Wheeler 1907; Sjöstedt 1907; Hegh 1922; Bugnion 1927). The gardens are quite distinct from the rest of the nest, which is constructed in quite a different manner. They present a picture of complex reactions to complex

stimuli. Fungus-growing behavior is confined to this subfamily of termites. Examples of nest-building behav'or patterns characteristic of higher taxonomic categories of birds are given by Chapin (1917).

CASTES INVOLVED IN NEST CONSTRUCTION

The nests of the primitive Kalotermitidae are excavated or constructed by the nymphs of the soldiers and reproductive castes except for the original cell of the colonizing pair. It is probable that the Mastotermitidae follow

FIG. 6. Mounds of *Amitermes vitiosus* (?) Hill between Camooweal, Queensland, and Newcastle Waters, Northern Territory. Photograph through the courtesy of G. F. Hill.

the same rule. The situation among the Hodotermitidae is more obscure because the exact status of the darkly pigmented, eyed "worker" has not been definitely established. Among the Rhinotermitidae and Termitidae, the adult sterile worker has become differentiated through neoteinic evolution from the soldier nymph (Emerson, 1926, 1935; Hare, 1934). However, it is quite common to find smaller worker-like forms, fully pigmented and with the abdomens containing the same materials as those found in the adult workers. These individuals seem to be nymphs of workers or soldiers and their behavior is the same as that of the adult workers as far as is known (Emerson 1926). It is thus probable that the worker-like nymphs of the soldiers have the same complex behavior patterns as the workers, and function in the construction and nutrient activities. Mature soldiers, however, never seem to assist in nest building. Snyder (1920, p. 190) states that the nasute soldier uses the fluid exuded from the beak in making shelter tubes, but I am convinced that this statement is an error. It has not been demonstrated that the nymphs of the reproductive castes of the Rhinotermitidae or Termitidae ever take an active part in gathering much food or constructing

the elaborate nests. The construction of the original cell in wood or dirt by the colonizing pair, however, indicates that nesting behavior has not been wholly inhibited in the reproductive castes.

Spencer (1893) attempted to explain the differences between the behavior of the reproductive caste and the worker in the Hymenoptera as a loss of instinct on the part of the reproductive caste, the primitive species having the instincts before caste divergence took place. Holmes (1911) points out

FIG. 7. East face of mounds of *Amitermes meridionalis*. Photograph through the courtesy of G. F. Hill.

the weakness of this contention, which is further demonstrated in the behavior evolution occurring long after the establishment of the adult sterile worker caste among the termites.

ECOLOGICAL FUNCTIONS OF THE NEST

The nest would seem to be of value to the termites as a means of controlling certain variables in the environment or for allowing sufficient elasticity of conditions to enable the insects to avoid certain environmental extremes. In order to test the variation in temperature within nests in relation to variations in the environment, two nests of *Nasutitermes corniger* on Barro Colorado Island were chosen. One was located in a clearing on a small stump, the base in contact with the ground and the top two feet from the ground. The stump was under a banana tree and was forty feet from the edge of the forest. The greatest diameter of the nest was one foot. A short thermometer (4 in.) was placed in a hole stoppered by a cork. The hole was about 1 inch wide and the bulb of the thermometer was 5½ inches from the surface. The other nest was attached to a small vine in the forest about twenty feet from the edge of the clearing. The forest roof was about fifty feet high. The bottom of the nest was 1½ feet from the ground. The nest was 2 feet high and 1½ feet in greatest diameter. A hole about 1 inch wide was dug into the nest so that the bulb of the thermometer (matched with the

TABLE 1. TEMPERATURE AND LIGHT MEASUREMENTS THROUGH A DAILY CYCLE IN THE ENVIRONMENT AND IN CLEARING AND FOREST NESTS OF *Nasutitermes corniger* IN PANAMA.

Time	Clearing				Forest				Remarks
	Nest Temp. °F.	Shade Temp. °F.	F. C. Light on Nest	F. C. Light in Sun	Nest Temp. °F.	Shade Temp. °F.	F. C. Light on Nest	F. C. light in Sun Fleck	
10 A.M.	79.0	83.5	1300	10500	80.5	82.0	25	200	Sunny
11 A.M.	86.0	86.0	11500	11500	81.0	81.0	20	5000	Sunny
12 M.	87.0	85.0	8500	8500	81.5	79.5	30	5500	Sunny
1 P.M.	90.0	86.0	9500	9500	82.5	79.5	10	30	Partly cloudy
2 P.M	92.0	79.5	800	800	83.0	77.5	¼	—	Cloudy
3 P.M.	92.0	79.5	950	950	83.0	77.0	5	—	Cloudy
4 P M	91.0	80.0	195	195	83.0	78.0	0	—	Light rain
5 P.M.	91.0	79.0	160	160	83.0	78.0	0	—	Light rain
6 P.M.	89.0	77.5	50	50	83.0	78.0	0	—	Light rain
7 P.M.	88.5	77.5	0	—	82.5	77.0	0	—	Rain stopped
8 P.M.	87.0	74.5	0	—	82.5	74.5	0	—	Stars out
9 P M.	84.5	74.5	0	—	82.5	74.0	0	—	Stars out
10 P.M	83.5	74.0	0	—	81.0	74.0	0	—	Stars out
11 P.M.	82.0	74.0	0	—	80.5	74.0	0	—	Stars out
12 P M.	82.0	74.0	0	—	80.5	74.0	0	—	Stars out
1 A M.	82.0	73.5	0	—	81.0	74.0	0	—	Stars out
2 A.M.	81.0	74.5	0	—	79.0	74.8	0	—	Cloudy
3 A.M.	81.0	74.5	0	—	79.0	75.0	0	—	Stars out
4 A.M.	80.5	74.5	0	—	78.5	75.0	0	—	Stars out
5 A.M.	79.0	74.5	0	—	78.5	75.0	0	—	Stars out
6 A.M.	79.5	75.8	5	5	78.5	75.0	0	—	Cloudy
7 A.M.	80.0	77.0	450	450	78.5	76.0	10	--	Cloudy
8 A M	80.5	78.0	600	1800	78.0	77.5	50	300	Sunny
9 A M	81.0	79.0	1100	1200	78.5	77.0	15	15	Cloudy
10 A M	82.0	80.5	1600	1650	78.5	78.0	20	25	Cloudy
11 A M	83.0	83.0	2500	3000	79.0	79.0	25	35	Dim sun

thermometer in the clearing nest) was 6½ inches from the surface and the hole was stoppered. Measurements (Table 1) were taken approximately on the hour on September 2d and 3d, 1935, for a period of over 24 hours. Light readings (in foot candles) were taken by means of a Weston illuminometer. In general the measurement of illumination in the sun in the clearing showed little difference from that on the nest. A light rain fell intermittently from 2.30 to 7.00 P.M. and doubtless influenced the temperature and illumination records.

One concludes from these measurements (Table 1) that (1) the direct sun rays on the nest raise the internal temperature above the shade temperature of the surroundings, and (2) that the temperatures follow the daily rhythm of the external temperatures, but lag behind the rising and falling external temperatures and do not reach the extremes found outside the nest. Of course, the sun temperatures outside the nest which reached maxima above 120°F. (the limit of the thermometers available) were far in excess of any internal nest temperature, and the nest temperatures measured above the maximum shade temperatures were doubtless due to the direct rays of the sun.

It is thus possible to say that the nest structure partially protects the

termites from the temperature extremes found outside of the nest. Cowles (1930) measured external and internal nest temperatures in the nests of *Trinervitermes trinerviformis* in Natal and his table shows the same tendency in these mound nests. Subterranean nests probably follow the temperature cycles of the surrounding soil very closely and this feature may be considered one advantage of such a habitat. Although it is possible that there is some migration of termite workers and soldiers influenced by tem-

FIG. 8. South end of mounds of *Amitermes meridionalis*. Photograph through the courtesy of G. F. Hill.

perature variations within the nest (Holdaway, 1935) and between the nest and the ground, the queen is of necessity usually confined to the royal cell and the young nymphs are seldom found far from the center of the nest.

Of probably greater importance than temperature is the control of humidity within the nest as compared to the extremes to be found in the external air. No measurements of nest humidities have been made, but it is safe to assume that the occupied nests of the Rhinotermitidae and Termitidae have almost a saturated air humidity (See Cowles, 1930, p. 23). The reaction of these termites to humidity gradients (Williams 1934; Emerson, unpublished experiments) indicates that they move away from dry air toward saturated air and that they die from even a brief exposure to dry atmosphere. Species of the Kalotermitidae often show more toleration to dry atmosphere and also often do not move from dry air to saturated air when exposed to humidity gradients. It is this dependence upon saturated or nearly saturated humidity that is probably the most important reason why the rhinotermitids

and termitids are typically soil termites and, when above the surface of the soil, they typically construct nests and tunnels which maintain humid conditions not very different from the subterranean habitat. Slight differences in the moisture requirements between *Reticulitermes hesperus* Banks and *R. tibialis* Banks demonstrated by Williams (1934) make it reasonable to suppose that such differences may often determine the ecological distribution of the species. Even the desert termites, however, so control the humidity of the air surrounding them that they live in an atmosphere close to saturation. The case is different in the Kalotermitidae, however, and the ability of *Cryptotermes*, for example, to live in the wood of dry furniture is doubtless linked with a greater toleration to dry atmosphere than is found in the species of Rhinotermitidae and Termitidae.

FIG. 9. Rain-shedding dirt-carton nest of *Amitermes excellens*. A wood-carton nest of *Nasutitermes guayanae* is visible on the right side of the trunk.

Other factors that may be of some importance to termites are the oxygen necessities and the elimination of carbon dioxide. Williams (1934) reports positive experiments upon these factors. The ventilation pores in the nests of *Apicotermes* may function for the exchange of gases. It may well be that the elimination of carbon dioxide may determine the site of the nest to some extent. Soil heavily soaked in water or with the surface flooded would certainly not offer a favorable site for a termite nest and the tendency to construct mounds and arboreal nests may enable termites to live in otherwise unfavorable localities.

The termite literature abounds in references to the avoidance of light. The only definite orientation with response to light of which I am aware among termites is the photopositive reaction of the winged imagoes during the first part of the colonizing flight. I have myself reported (Emerson 1929) a "negative phototropism" of the imagoes before the flight starts and after it is finished, but more accurate experimentation indicates that the pho-

topositive reaction is only present for a short time and the insect is neutral to light at other times. This neutrality does not apply to heat and to increased evaporation, however, and the actions usually interpreted as negative responses are probably the result of these other factors which are so often

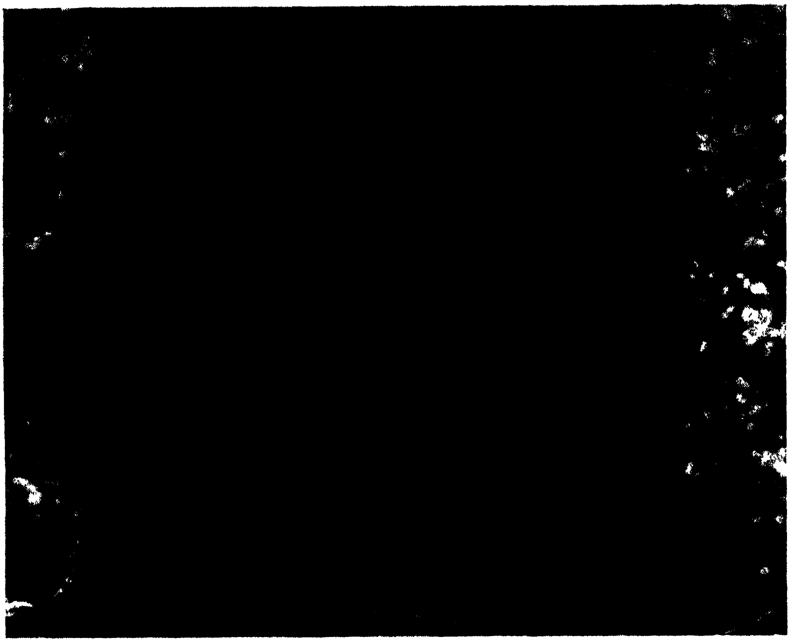

FIG. 10. Detail of rain-shedding projections of nest of *Amitermes excellens*.

closely associated with increase in the intensity of light. I should consequently not interpret the construction of nests or tunnels as the result of photonegative behavior.

Another factor emphasized in the literature, particularly by Bugnion (1927), is the construction of the nests for the protection of the inhabitants from predatory enemies. It is certainly true that exposed termites form ready prey for wasps, ants, spiders, lizards, and other predators. Ants in particular have doubtless been enemies of termites for many ages and some species prey only upon termites (Wheeler 1936). Experiments as yet unpublished indicate the ability of the soldiers to combat these enemies in comparison with the defensive ability of the workers. The evolution of the soldier caste has doubtless been guided by the selection of efficient means of defense against predators and it is quite conceivable that the nest-building patterns have also been selected because of their value in protecting the colony from attack. I have never observed a direct influence of the presence of predators upon construction which cannot better be explained as a response to other factors, however, and I am of the opinion that any such direct re-

sponse to ants as that postulated by Bugnion (1927, pp. 14, 30) needs critical verification. A few predators are especially adapted to overcome the protection the nest affords. The modified forefeet of the spiny anteater, pangolin, aard vark, and New World anteaters enable these animals to invade the hard nests of termites. The cylindrical sticky tongues of these phylogenetically diverse mammals are astonishingly efficient in penetrating the complex system of cells in the termite nest. The prehensile tail, found in the tamandua, silky anteater, and some pangolins, enables these predators to reach the arboreal nests. The remarkable adjustments of these specialized termitophagous mammals only serve to emphasize the value of the nests as protection from general predators and indicate how strong the selection pressure was to influence the evolution of such striking convergent adaptations.

Not only is the nest a protection against animal predators, but it is also a protection from harmful fungi. Laboratory colonies removed from nests often succumb to molds which seem to be effectively controlled under natural conditions.

SELECTION OF THE NESTING SITE

One might suppose that the selection of the nesting site involved no more behavior response than is found in seeds scattered by the wind. It is true that the flying termites scatter in all directions and a very large proportion alight in unfavorable locations. I have seen thousands entrapped in the surface of a river where fish were rapidly devouring them. I have seen thousands die of heat and evaporation on the hot sands of dunes. I have seen paired couples entering crevices in a wharf which was soon to be inundated by a rising tide. Certainly the mortality is high during the colonizing flight. On the other hand, the colonizing pair in *Termes inquilinus* and *T. fur* would seem to select the nests of *Constrictotermes cavifrons* and *C. cyphergaster* respectively for their nesting site and there are other indications that the imagoes are not wholly subject to chance. There is strong evidence that considerable powers of selection are manifested, not so much by the colonizing pair as by the workers after the colony has developed. The migration of an entire colony of *Nasutitermes costalis* including the royal couple and many termitophiles has been reported (Emerson, 1929). The process of moving the nesting site will rarely be seen by human eyes, but migrations must be assumed when nests are found in locations where the royal pair could not have excavated their original cell. Such is the case for every nest of *Constrictotermes cavifrons* seen in the British Guiana forest (Fig. 14). These nests were invariably found on living trees with smooth bark, and in nine out of ten cases the tree slanted at an angle to the ground. The living bark was not invaded by the termites. The evidence seems convincing that all these nests were established through the migration of the entire colony. The uniformity of the nesting site in this species indicates behavior reactions

of which we know practically nothing. How blind, rather small insects can select a tree with smooth bark rather than rough, the under side of a slanting surface rather than the upper, and then, after at least preliminary construction by hundreds of individuals, stimulate the entire colony including the grossly physogastric queen to move to the new site, is difficult to analyze. It is not surprising that uncritical commentators fall back upon anthropomorphic explanations of such facts.

Especially in arboreal nests, height above the ground may be characteristic of the species or genus. Of the nests which I have studied in the New World, *Nasutitermes costalis, N. ephratae, N. surinamensis, N. wheeleri, N. acajutlae, N. corniger, N. pilifrons, N. guayanae, N. similis, N. columbicus, Constrictotermes cavifrons, Anoplotermes (Speculitermes) arboreus, Amitermes excellens* and *Microcerotermes arboreus* build at varying heights from the ground. The last four species build dirt carton nests and the others build of wood carton. Other species seem to be limited to sites at most only a few feet above the ground, such as *Anoplotermes silvestrii, A. banksi, A. brevipilus* and various species of *Termes* and *Armitermes*. Every gradation from these sites to subterranean locations may be found, but the range for each species seems to be fairly characteristic, although there may be considerable variation within each species.

Nests may be built quite rapidly. A nest of *Amitermes excellens* Silvestri was constructed about 50 feet from the ground on a tree near the Kartabo laboratory between September 15, 1919, and June 1, 1920. This nest was about 3 feet long, 1 foot wide and ½ foot thick. A colony of stingless bees had partly occupied the interior. I assume that the colony migrated to a new site in this case. Nests enlarged in proportion to the growth of the colony would doubtless grow more slowly.

NEST DIVERGENCE WITHIN A GENUS

It has often been observed that adaptive modifications are more conspicuous as one ascends in the ranking of the animal group. Adaptations between families are more obvious than between genera, and adaptations between genera are more obvious than between species of the same genus. One explanation of this difference in different categories may be that genera arise through further speciation of adapted species, while less adapted species may not survive through the ages of competition. Striking adaptive divergence probably takes a long time under fairly strong selection pressure, while speciation mechanisms may operate with slight selection (Wright, 1932, p. 363). If the mechanisms of evolution are operating to produce adaptive behavior in the same way that they operate to produce adaptive physiological interaction and structural growth, we may expect to find this rule illustrated in the nesting behavior of termites.

The general outline of family differences in nests has already been pre-

sented. Many genera show similar nesting tendencies between various species, notably the dirt carton nests of *Microcerotermes*, the wood carton arboreal nests of most species of *Nasutitermes*, *s. str.* (Figs. 3, 4, 9), the mushroom-shaped nests of *Cubitermes* (Fig. 11), and the perforated nests of *Apicotermes*.

It is also possible to show striking divergence between the nests of species of the same genus, notably in the genera *Nasutitermes*, *Anoplotermes*, and

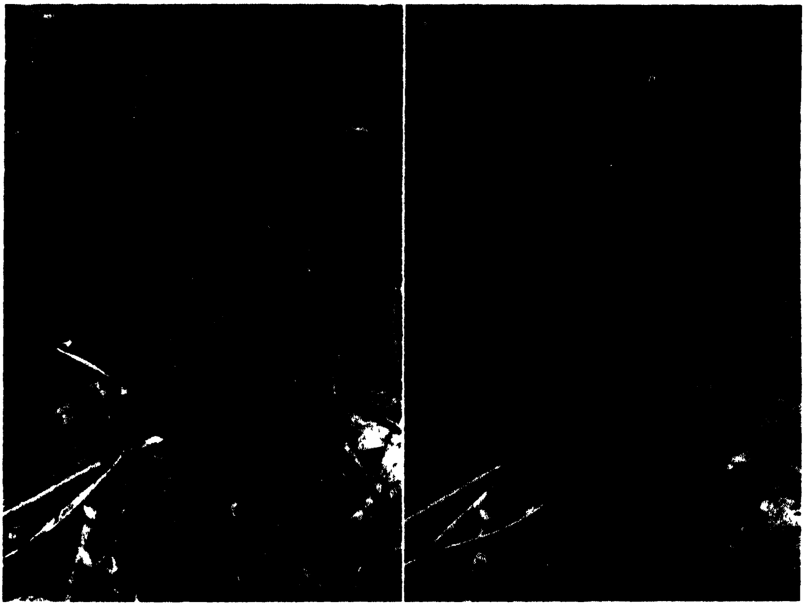

FIG. 11. Mushroom-shaped dirt-carton nest of *Cubitermes loubetsiensis* Sjöstedt, Medje, Belgian Congo. The cap with peripheral projections sheds rain from the stem. The height measured 44 centimeters. The vertical section shows the connecting holes between the cells and the queen in the middle just above the narrow part of the stem. Photographed by Herbert Lang.

Apicotermes. I have selected the genus *Amitermes* as the best example known to me which illustrates such divergence as well as striking adaptive nest modifications.

Amitermes is a genus found in every zoogeographical realm, but in general it is found in the tropics and only in the warmer portions of the temperate realms. As a genus, it seems particularly adjusted to dry regions, many more species being found in such regions as the southwestern semi-deserts of the United States than in the rain-forests of the tropics.

The majority of the species do not build definitive nests above the ground which lend themselves to photography. Examples of such inconspicuous nests are those of *A. beaumonti* Banks in Panama, *A. wheeleri* (Desneux) in Texas, and *A. santschii* Silvestri in north Africa.

A number of species, particularly in Australia, build mounds above the ground which may be conspicuous features of the landscape (Figs. 5, 6). Illustrations of such nests of *Amitermes* are to be found in Hill (1922, 1922a, 1935), Froggatt (1905), Mjöberg (1920), Hegh (1922), Snyder and Zetek (1934), Emerson (1937a). It will be noted upon examination of these various photographs that there is a fair amount of variation in the shapes of the nests within a given species, but it is also obvious that characteristic distinction between the different species exists and in several instances the species may be easily recognized by means of the nest alone.

From many viewpoints, the most remarkable nest known is that of *A. meridionalis* (Froggatt). This nest is the famous "magnetic" nest found in north Australia (Figs. 7, 8) which is figured by Froggatt (1905), Hegh (1922), Hill (1922, 1935), and Emerson (1937a). Hill (1935) questions the determinations of the nests described and figured by Saville-Kent (1897, 1897a) and Mjöberg (1920). The largest of the "meridian" nests are about 12 feet high with a north-south length of about 10 feet and an east-west width of about 3½ feet at the base in the middle. Hill (1935) gives the most complete and accurate account of the geographical and ecological distribution, the shape and orientation of the nest, and a discussion of the theories to account for the peculiar orientation. Hill states (private correspondence):

> I have thought that the probable reasons for the mounds being built with the long axis approximately north and south is to obtain the maximum total amount of solar radiation during the winter months, and the minimum during the heat of the day in summer.

It would seem to me that the explanation probably will ultimately be found in the control of temperature, although theories placing emphasis upon humidity and wind have already been proposed. Not only is the explanation of the adaptive value of such a nest important, but a knowledge of the factors to which the termites are reacting directly would add much to our concept of nest evolution.

Andrews (1927) and Dreyer and Park (1932) discuss ant nests of the genus *Formica* which are oriented with reference to light and give measurements of light and temperature. These ant nests have their broadest face toward the south and the most direct rays of the sun. The difference in the orientation of the nests of *A. meridionalis* may very likely be owing to their tropical location and possibly to the greater extremes of temperature to which they are subjected.

In sharp contrast to the mound nests of the more arid savannahs, *A. excellens* constructs nests on the sides of surrounding trees in the rain-forest of British Guiana. Galleries covered the entire trunk of a dead tree in an old clearing near the Kartabo laboratory (Figs. 9, 10). The tree was covered to a depth of about 8 inches and to a height of about 45 feet. The material was a sandy-dirt carton which easily crumbled in the hand. The exterior

was covered by numerous finger-like projections extending downward and outward. Upon breaking these projections they proved to be hollow and were always occupied by a few termites. The function seems to be for the shedding of rain water during heavy tropical showers. In this particular

FIG. 12. Rain-shedding dirt-carton nest of *Cubitermes subarquatus* on a tree at Medje, Belgian Congo, composed of a series of caps with peripheral projections. Photographed by Herbert Lang.

FIG. 13. Nest and rain-shedding, chevron-shaped structures of *Procubitermes niapuensis* on a tree at Niapu, Belgian Congo. Photographed by Herbert Lang.

locality the annual rain fall was around 110 inches. Heavy rain fall (5 to 8 inches) of short duration was not uncommon.

When these structures are first started on the side of a tree, a long vertical covered gallery is built on the trunk, and side branches are built in a peculiar parallel arrangement inclined downward on the tree at an angle of about 45° to form a "herring bone pattern" (Emerson, 1937a, p. 246). The function of this construction is also probably the efficient shedding of rain which descends the tree trunk.

CONVERGENT EVOLUTION WITHIN A SIMILAR HABITAT

The adaptive significance of a modification is more convincing if it is possible to show that organisms from stocks not possessing the modification have separately evolved a similar adjustment when subjected to natural selection within a similar habitat. The function of the finger-like projections on the nest of *Amitermes excellens* becomes more clear if similar nest structures appear in unrelated termites typically found in or near rain-forests. Convergence of rain-shedding structures may be demonstrated in three different subfamilies of the Termitidae including the Amitermitinae already discussed. Without doubt these subfamilies had no common ancestor from which they could have inherited such a pattern.

The Termitinae include several African genera which can be arranged in a series possibly illustrating an evolutionary sequence. *Cubitermes* often constructs a unique mushroom-shaped nest (Fig. 11), the specific variations of which have been well illustrated by Sjöstedt (1913), Hegh (1922), and Emerson (1928). These nests show definite generic similarity but at the same time show specific differences. The majority are capped by an umbrella-like structure, convex on top and projecting outward at the periphery in such a way as to shed rain from the top of the nest. Finger-like projections, quite similar to those described on the exterior of the nest of *Amitermes excellens,* often extend around the edge of the cap. The nest of *Cubitermes subarquatus* Sjöstedt (Fig. 12), found in the Congo rain-forest, deviates from the mushroom-shaped form found in more open country by appearing to be a succession of caps, one above the other. This nest type might easily have evolved from the mushroom type. The remarkable nest (Fig. 13) of a species from the Congo rain-forest, *Procubitermes niapuensis* Emerson, belongs to a closely related genus. The termites build a series of hollow, chevron-shaped, dirt-carton structures extending for some distance above the nest proper on the side of the tree trunk. Mr. Herbert Lang, who examined and photographed the nest, is of the opinion that the ridges function for the shedding of rain (Emerson 1928).

In the rain-forest of British Guiana, still another nest exhibits rain-shedding modifications (Fig. 14). The species is *Constrictotermes cavifrons* belonging to the Nasutitermitinae. The entire structure sometimes reaches a length of about 3 feet. It is attached for most of its length to the side of a smooth-barked live tree. A discussion of other features of this nest is to be found in the preceding pages. Pertinent to our present consideration is the series of solid, sharp carton ridges which extend over the surface of the nest and continue downward at an angle along the tree trunk at the sides of the nest. These ridges are also built some distance above the nest and form a series of chevron-shaped structures which remind one of similar structures in the nest of *Procubitermes niapuensis* (Fig. 13). In the case of the nest of *C. cavifrons,* however, the ridges are more numerous, are sharp and solid,

and are built over the surface of the nest. The surface of the bark is cleaned of lichens and similar outgrowths between the ridges, and an open passageway is left above the nest which allows ease of travel up the tree. I have observed the nest during a heavy shower and there is no question that the

FIG. 14. Profile and detail of edge of nests of *Constrictotermes cavifrons* on smooth-barked slanting trees at Kartabo, British Guiana. Sharp, solid, rain-shedding ridges extend above the nest on the tree trunk as well as over the surface of the nest and down the sides of the trunk. The termites have bridged over the ridges as they enlarged the nest (upper right). The hanging basal part of the nest (lower left) is composed of stored food and is occupied by the semi-parasitic termite, *Termes inquilinus.*

ridges deflect the sheet of water descending the trunk of the tree in such a manner as to keep the nest relatively dry and moistened only by the drops which fall directly upon it. Hingston (1932) describes this nest and arrives at the conclusion that the ridges "shoot the water forward and outward clear of the nest." My observations did not indicate that the water was "shot" outward, but that the stream was deflected to the side and ran down the trunk without wetting the nest. Hingston also describes an experiment in which he cut 18 ridges above the nest, allowing the water to run into the nest. He

states that the water moistened and softened the earth carton of which the nest is composed. In the fourth week following the injury to the ridges, the termites started to repair and replace the ridges and had completed eight during the sixth week when the observations ceased. This experiment of Hington's is most interesting because it indicates that the termites may react to the percolation of the rain-water into their nest.

DISCUSSION

Because the insects in the experiment outlined above have successfully met an emergency, Hingston classifies this behavior as intelligence (also see Imms 1931, p. 16). A cut in the finger is an unusual event for the cells involved and adaptive clotting of blood followed by the growth of tissues reacting to complex factors result (Arey 1936), but the physiologist would hardly be inclined to say the reacting cells were intelligent. Such somatic physiological activity is known to be influenced by hereditary factors as evidenced by the genetics of haemophilia. The termite behavior recorded by Hingston seems to me to offer a significant parallel.

Unless the nesting behavior be largely hereditary, there is no more phylogenetic significance in its evolution than in the evolution of human architecture. Human architecture seems to rest wholly upon a capacity for "conditioning" and intelligent response to environmental and esthetic factors. From the standpoint of behavior analysis, it is in sharp contrast to termite architecture. Both types of behavior, of course, may be of fundamental importance to the biological success of the species.

The tendency to resort to anthropomorphic explanations is noteworthy in observers who are astonished by the remarkable complexity of termite life. Maeterlinck (1926, 1928) is especially prone to such generalizations. Bugnion (1927) and Imms (1931, p. 102) resort to the "lapsed intelligence" theory of Lewes with its Lamarckian implications to explain the origin of "instincts". All of the references to termite "intelligence" known to the author carry strong anthropomorphic connotations.

Kemner (1929) has given a classification of the termite nests which he studied in Java and also discusses the systems of classification used by Holmgren (1906). In certain respects I find myself in agreement with Kemner's phylogenetic arrangement—namely in treating the kalotermitid-type nest as the most primitive and postulating the evolution of the rhino-termitid-type from the kalotermitid-type. In the arrangement of the phylogenetic sequence of the various types of termitid nests, however, I cannot agree with Kemner because the arrangement is opposed to phylogenetic sequence based upon a study of the morphological characters of all the castes (Hare 1937). It would seem to me that all correlated evidences of phylogeny would have to be considered and certainly comparative morphology cannot be ignored, not because behavior or physiological characteristics are

less important than morphological characteristics, but the significantly correlated characters which have been studied from a phylogenetic viewpoint are largely morphological at the present state of our knowledge. Without breaking away from the deduced phylogenetic history of the major groups of termites, one may assume that the most primitive termitids were ground and log dwellers not differing greatly from the rhinotermitids in their nesting behavior. Many morphologically specialized termitids have not deviated much from this basic behavior type. Radiation, however, may conceivably have occurred in several directions leading to simple ground excavations, mound nests, fungus-garden construction, arboreal dirt nests, arboreal wood-carton nests, and other more specialized types, a few of which have been discussed in the preceding pages. It is not necessary to assume that any of the more basicly specialized termitid-type nests were derived from any other specialized type and there is much evidence against this hypothesis. Among certain closely related groups such as the species of *Apicotermes* and species of *Cubitermes* and *Procubitermes,* one may postulate evolutionary sequences which fit the morphological data, but a postulate that *Microcerotermes*-type nests evolved from *Nasutitermes* (= *Eutermes*)-types and that the fungus-growing behavior was an aftermath of the type of nest-building behavior of *Microcerotermes* seems to me wholly out of line with a considerable body of facts upon which the phylogenetic arrangement of these groups is based.

The separation of analogous from homologous morphological structures through the maze of genetic modifications, physiological influences, growth patterns, degenerative changes, and convergent adaptations, is a difficult task. With increasing knowledge of connecting links and a better understanding of the principles of embryology and of evolution, we are enabled to rectify many of the mistaken conclusions of the past. However, in spite of the fact that the principle of homology has been applied to the evolution of termite nests, I think that the best available evidence is a parallel series of homologous morphological structures. Whether homology is assumed for structure, for behavior or for physiological action, it would seem to rest upon a similar genetic basis manifesting itself through successions of enzymic effects and physiological actions and interactions (Wright 1934, p. 33). That behavior may be dependent at times upon local chromosomal influences has been demonstrated by Whiting (1932) in his studies of the reproductive reactions in sex mosaics of the parasitic wasp, *Habrobracon.*

I have cited one instance of degenerative evolution of nesting behavior in the case of *Termes inquilinus.* Degenerative evolution of behavior may have occurred in numerous instances, but few cases are associated with sufficient data to justify a reasonable conclusion. Degenerative evolution is an example of a negative and usually non-adaptive directional tendency that has been a stumbling block for many evolutionary theorists. Modern ge-

netics, however, has shown that mutations are often degenerative in their manifestations, that they may occur at statistically predictable rates, that species characters are usually an outgrowth of gene and chromosome combinations, and that natural selection is probably responsible for keeping wild populations from exhibiting degenerative tendencies of functional characteristics. "Mutation pressure" resulting in degenerative effects might produce a degenerative evolution if selection pressure for a particular structure or function were removed (Wright 1929; Darlington 1936). Degenerative mutations would seem to have more effect in small interbreeding populations. Another positive influence has been postulated (Wright, 1929) in the probable fact that "each character is affected by many genes and each gene affects many characters" (Wright, 1934, p. 30). Thus selection probably does not act upon the single effect, but selects genes and gene combinations which result in a sum total of favorable effects. Consequently a gene or system of genes causing degeneration may be selected for other beneficial effects, particularly if a former beneficial effect has been lost or decreased through a change in the environment.[1] It is thus possible to explain known evolutionary trends on the basis of modern genetic theory without recourse to Lamarckism. Non-adaptive evolution is possible (Wright 1932, p. 363) and it is not necessary to assume adaptive value for every specific character. The multiple effects of genes also give a reasonable explanation of non-utilitarian vestigial structures and recapitulative tendencies. Sudden complete losses of the hereditary basis of complicated structures would probably indicate such gross genetic changes that other vital functions would be affected. It is more probable under natural conditions that the old heredity has merely become overlaid by new heredity suppressing or modifying structures or actions (Wright 1935, p. 105). Needham (1930) emphasizes the opinion that "organs are only recapitulated in so far as they are necessary for the development of the ones which are required in the ontogeny in question, and all the other old ones disappear." Although recapitulative structures and actions may often have functions, it seems difficult to believe all cases are functional and Wright's explanation allows for the possibility of recapitulation of non-functional organs or actions.

I have searched my experience and the literature for a case illustrating vestigial behavior among termites, but I am unable to offer a single instance which is worthy of consideration. In a sphere far removed from the insect world, however, I wonder whether the rather futile action of dogs in scratching dirt following defecation may not be considered an example of behavior which has undergone phylogenetic degeneration, but is still visible as a vestigial pattern (see Enders 1935 for an account of specific differences in faecal behavior of Panamanian cats).

[1] Wright, in commenting upon this statement, adds: "The type allele in each series is that which has the most favorable net effect on all characters. If one character loses in importance relative to others, there will be a shift in the alleles in many series with degeneration of the character losing importance as a consequence of the increased development of the others."

The foregoing discussion emphasizes the phylogeny of inherited species behavior patterns, but I see no reason why individual behavior involving modifiability through experience (Emerson, 1933) may not be characteristic of termites. Such behavior seems to be relatively unimportant in the phylogenesis of the species patterns discussed in this paper. Ranges of variation in the inherited pattern may also be demonstrated under identical environments, and different environments will doubtless bring about variation in the patterns with the same heredity. A better understanding of the ontogenetic development of both genetically and environmentally induced behavior is highly pertinent. These problems await future investigation.

SUMMARY

1. Termite nests may be used as examples of behavior evolution because they are morphological indications of behavior patterns, they express the behavior of a population, the patterns are hereditary, there is a natural control over any Lamarckian influence, evolutionary sequences are available, adaptive modifications may be demonstrated, and coordination mechanisms may be partially analyzed.

2. Wood-eating roaches excavate galleries in wood but make no constructions.

3. The Kalotermitidae excavate wood and construct partitions, indicating responses to humidity and mechanical or chemical factors.

4. The Mastotermitidae exhibit a quantitative advance in nest construction compared to the Kalotermitidae.

5. The Hodotermitidae show a further advance with subterranean nests, elaborate carton construction, and food storage.

6. The Rhinotermitidae have separately evolved subterranean adjustment and in some species show building activities in response to social factors as well as physical factors.

7. Excavated subterranean nests of the Termitidae exhibit the influence of mechanical and spatial factors.

8. Materials used for construction may be dirt, wood, or excrement, cemented by saliva or anal excretions.

9. Structures may include covered tunnels, roads, rain-shedding projections and ridges, nests of characteristic size and differentiation, ventilation pores in the walls, stored food, and fungus gardens.

10. Sterile workers and nymphs of sterile soldiers and workers construct the nests in the Rhinotermitidae and Termitidae.

11. The ecological functions of the nest are control of temperature, control of humidity, and protection from predators and harmful fungi, all enabling the termites to live in otherwise uninhabitable niches.

12. The nesting site may be selected partly or wholly by the colonizing pair, but often is selected by the workers and is followed by a colony migra-

tion. Height of the nest from the ground may be fairly characteristic of the species.

13. Different species within a genus show great divergence in nesting behavior. Species of the genus *Amitermes* have subterranean nests, mound nests, arboreal nests, nests oriented with reference to the sun, and rain-shedding constructions.

14. Convergent evolution of rain-shedding constructions has occurred in the Amitermitinae, Termitinae, and Nasutitermitinae.

15. A discussion of "intelligence," correlation of morphological and behavior homologies, degenerative evolution and "vestigial" behavior is included.

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PHYSICAL ECOLOGY OF THE FIREBRAT, *THERMOBIA DOMESTICA* (PACKARD)

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INTRODUCTION

The firebrat, *Thermobia domestica* (Packard), is one of the most common household pests, although not recognized by many people. It is largely nocturnal in its habits, especially if food is plentiful. Being quick and active the insect scurries to shelter behind some object or into some crevice when disturbed or when lights are turned on in a dark room.

Although widespread, this thysanuran has not been studied very intensively, which lack of interest is due largely to the belief among scientists as well as laymen that the life cycle occupies a period of two to three years. The detailed study of the habits and ecology of this pest furnishes much needed information.

SYNONOMY

Thermobia domestica (Pack.)
- *Lepisma domestica* Pack. 1873
  - Packard-5th. Ann. Rpt. Peabody Acad. Sci.: 23-51
- *Lepismodes inquilinus* Newm. 1863
  - Newman-Zoologist f. 1863:8496
- *Lepisma furnorum* Rovelli 1884
  - Rovelli-Zoo. Anz. 8:60
- *Termophila furnorum* (Rovelli) 1887
  - Grassi-Bul. Soc. Ent. Ital. 19:58
- *Thermophila furnorum* (Rovelli) 1889
  - Grassi & Rovelli-Bul. Soc. Ent. Ital. 21
  - Oudeman-Tijdschr. v. Ent. 22:425-32
- *Thermobia domestica* (Pack.) 1890
  - Bergroth-Ent. Amer. 6:233
  - Packard-Ent. Mon. Mag. 30:155-6

DISTRIBUTION

The firebrat has become very widespread in the tropical and temperate zones. It is likely to be found even in cold regions where heated habitations of man are common. Originally it must have been a warm climate insect. Apparently it received the common name, firebrat, because of its habit of living about outdoor bake ovens in England, where it was well known long before it received its scientific appellation.

FOOD HABITS

It is reported in much of the literature that the firebrat prefers starchy foods of many kinds. Damage to books, records, and other starchy paper materials, especially those having a glazed finish on starchy cloth, and cereal products such as white flour are cited frequently. Very few workers mention

that the insect feeds also on foods rich in protein content, although their cannibalistic habits are mentioned by several. A few observers have emphasized the importance of proteins in the diet of *Thermobia*. Both nymphs and adults feed readily on exuviae, eggs, dead bodies, and even weakened or injured individuals that are unable to resist attack. Investigations of the nutritional requirements of the firebrat are in progress.

METHODS OF HANDLING

The insects were observed and reared in controlled temperature chambers. The relative humidity was regulated by using saturated salt solutions containing an excess of salt, except for the 100% condition, which was obtained by using distilled water. The relative humidity in the containers was determined from time to time with a dew point hygrometer. The salt solutions were placed in pint glass top fruit jars and the insect cages hung in the jars above the solution. These cage bottles were tied to the wire cover clamps on the outside of the jars with a soft piece of string, which pressed into the rubbers when the jars were sealed. The nymph and adult cages were wide-mouthed bottles 50 mm. wide and 70 mm. deep. The mouths of the bottles were 32 mm. wide. The eggs were incubated in vials. The bottoms of the cages were covered with a thin layer of beeswax and sand or other materials to produce a rough surface to enable the insects to gain a better foothold. At first strips of corrugated paper and later strips of paper towels were placed in the cages to serve as hiding and egg deposition places. The strips were long enough to reach across the cages, thus preventing sliding about of the paper. This was important in preventing injury, especially with the early instars.

The food consisted of whole wheat flour or Mead's Cereal, a prepared food of known composition, and dried lean beef. Beef relatively free of fat was desirable and was preferred by the insects. The addition of the shredded meat apparently produced a diet much superior to cereals alone. An excess of food was added at each feeding so that ample was present at all times. The food in the environments in which the humidities were 97 and 100% was placed on paper strips to facilitate removal. Frequently the insects scattered a portion of the food over the bottom of the cage. Small brushes were used to aid in removal of fungous growth and particles of food that adhered to the bottom of the cage. Rubbing a finger around the curved neck of the cage bottles to remove dust particles of food was sufficient to prevent escape of the insects.

The sealed jars were opened and the insects examined as frequently as necessary depending upon the environments and the information desired. The insects in environments in which humidities were 97 and 100% were examined and the food changed daily because of the excess moisture that accumulated in the food and the growth of fungi in temperatures below 37°

C. The insects could tolerate being sealed in the jars for extended periods. The longest period was 3 months during the summer at room temperature, when some of the cages contained as many as half a dozen specimens. No apparent injury was produced by the gaseous environment in any of the cages except with certain salt solutions which decomposed. Where this occurred, decomposition took place immediately on starting the test and not after extended periods.

It greatly facilitated determination of the sexes in the early instars before the ovipositor became visible from a dorsal view, to observe microscopically the reflection of the ventral surface of the abdomen in a mirror. The nymphs were placed in shell vials about one-half inch in diameter and cut to about the same height, and this container placed on the mirror held at an angle so that the reflection of the specimen could be seen.

EGG STAGE

Description. The eggs of *Thermobia* are soft, white, and opaque when laid although the chorion is transparent. The chorion soon hardens, becomes tinged slightly with yellow, and the opacity of the egg usually increases. The eggs typically are elliptical in shape, but may be slightly bean-shaped or roundly pointed at one end. They are about 1 mm. long and 0.7 mm. wide in the greatest dimensions. The chorion of the freshly laid egg is smooth and devoid of sculpturing. However, Adams (1933a, b) states that the chorion is shiny and smooth with sparce minute markings. On about the third day at 35° C. distinct markings appear on the chorion, apparently produced by the cells of the embryonic tissues that are in intimate contact with it. The embryo is visible through the chorion on about the fourth day. The portion of the egg not occupied by the body of the embryo appears to be filled with a rather clear fluid. The pigmented eyes are evident by the eighth day. By the ninth day the legs are visible and movement of the embryo when the egg is disturbed is discernible. The liquid contents appear to be absorbed on about the thirteenth, and hatching occurs on about the fourteenth day. Some wrinkling of the chorion may occur during the early stages of development, but in favorable environments is rounded out again toward the end of embryonic development.

Hatching. Emergence is effected with the aid of an egg burster on the anterior portion of the head and by pressure which breaks the chorion. In unfavorable environments, especially the dry ones, the nymphs may be unable to break the chorion or may die when only partially emerged. This may occur when only an antenna or as much as the head and thorax are external. Frequently the abdomen is not extricated until the first molt (Sweetman, 1934). This is true especially in dry environments.

Response to Temperature and Moisture. Eggs were exposed in temperature and moisture environments ranging from 20° to 50° C. and relative

TABLE 1. THE INCUBATION PERIODS OF *Thermobia* EGGS EXPOSED AT VARIOUS TEMPERATURES AND IN VARIOUS HUMIDITIES.

Temp. °C.	Relative humidity	Number of eggs	Number hatched	Percentage hatched	Incubation Period: Range in days	Incubation Period: Average number of days
20	77	32	0	..	.....	..
22	100	3	0	..	.....	..
22	77	38	0	..	.....	..
22	51	3	0	..	.....	..
22	32	5	0	..	.....	..
22	14	3	0	..	.....	.
24	77	14	3	21	74–80	77
27	100	16	11	69	42–45	44
27	97	8	7	88	41–47	44
27	77	13	12	92	42–48	46
27	56	17	14	82	41–49	45
27	32	9	7	78	46–51	48
27	12	14	7	50	44–50	46
29	100	25	16	64	31–35	33
29	97	22	20	91	29–36	33
29	85	20	18	90	31–37	32
29	77	21	19	90	31–34	32
29	62	21	18	86	31–38	33
29	56	21	20	95	30–34	32
29	32	25	21	84	29–32	31
32	100	24	19	79	18–23	22
32	96	23	20	87	21–23	22
32	77	29	26	90	18–22	20
32	64	9	8	89	21–24	22
32	52	13	11	85	19–22	21
32	32	24	19	79	19–23	22
32	12	20	19	100	18–24	21
37	100	25	23	92	11–15	13
37	96	16	14	88	11–13	13
37	85	8	8	100	14–15	14
37	76	157	146	92	10–14	12
37	51	19	14	74	11–15	13
37	48	13	12	92	11–14	14
37	32	20	19	95	11–13	12
37	12	15	13	87	10–14	12
40	100	14	9	64	10	10
40	96	27	23	85	9–10	10
40	85	13	12	92	9–13	11
40	83	12	21	100	9–10	10
40	76	8	5	63	11–12	11
40	54	36	31	86	9–11	10
40	12	5	4	80	10	10
41	96	6	6	100	9–11	10
41	76	5	4	80	9	9
41	54	9	6	67	8–10	10
41	32	10	9	90	10–11	10
42	100	16	6	38	9–10	10
42	96	36	26	72	8–11	9
42	85	16	13	81	8–12	10
42	76	19	17	95	7–10	9
42	50	17	15	88	9–10	10
42	32	6	3	50	10	10
42	12	4	2	50	9–10	10
44	100	5	5	100	7	7
44	96	10	8	80	7– 9	8
44	86	9	5	56	7–11	8
44	82	5	2	40	9	9
44	79	8	3	38	9–11	10
44	76	29	22	76	7– 9	9
44	50	11	11	100	7–10	9
44	32	14	10	79	9–10	10
44	12	5	4	80	9–10	9
47	100	11	2	18	11–12	11
47	83	9	9	100	9	9
47	76	56	39	70	8–15	11
47	50	18	17	94	9–10	9
47	32	1	1	100	9	9
47	12	9	0	0	.....	..
48	75	25	0	0	.....	..
49	75	24	0	0	.....	..
50	75	83	0	0	....	..

humidity of 12 to 100%. The eggs failed to hatch at 20° and 22° C., although some development occurred (Table 1). A large majority of the embryos developed to maturity at 24° C., but only 21% of the total number of eggs hatched. The nymphs from these eggs were very weak and died in a few days without molting. Further evidence of the injuriousness of this low temperature to the developing embryos is shown by eggs that were transferred to 37° C. after 41 days exposure at 24° C. Five eggs were transferred, three embryos developed, but only two hatched after 7 to 8 days' exposure at the higher temperature. One nymph was apparently normal and lived. Nymphs emerged from eggs exposed at 27°C. in 41 to 51 days. Above 27°C. a rapid reduction in developmental time occurred for each degree rise in temperature to 37° C., being 33 days less at this latter temperature than at 27° C. and over two months less than at 24° C. Adams (1933a) reported that 15 days was usually necessary for incubation of the eggs at 37° C. However, when the temperature was carefully measured in the immediate vicinity of the eggs, the average time was twelve to 14 days. About 14 to 15 days are necessary for embryonic development at 35°C. Above 37°C. the decrease in the length of the incubation period with a rise in temperature continued until the shortest period was reached at 44° C., where 7 to 11 days was sufficient. Exposures at 47°C. resulted in a lengthening of the incubation period to 8 to 15 days (Tables 1, 2). None of the eggs hatched above 47°, although some development occurred at 48° C. Short exposures at 48° C. were not always fatal. Eggs exposed at 48° C. for one week, then transferred to 37° C. hatched after 7 to 10 days exposure at the lower temperature. One embryo, well developed at a favorable temperature, hatched about a day after being exposed at 49° C.

No consistent effects of moisture are evident at the different temperatures in so far as shown by the length of the incubation period. When the per-

TABLE 2. THE AVERAGE DEVELOPMENTAL PERIOD AND THE AVERAGE PERCENTAGE OF HATCH OF *Thermobia* EGGS EXPOSED AT VARIOUS TEMPERATURES AND IN VARIOUS HUMIDITIES.

Temp. °C.	Average incubation period. Days	Average hatch. %	(x — n)y values
20		0	.
22		0	.
24	77.2	21.4	..
27	45.3	75.3	135.9
29	32.3	65.1	161.5
32	21.3	86.6	170.4
37	12.4	90.5	161.2
40	10.2	83.5	163.2
41	9.8	63.0	166.6
42	9.5	72.8	171.0
44	8.9	74.0	178.0
47	11.0	69.8	253.0
48		0	. .
49		0	. .
50		0	. .

centage of nymphs hatching is considered, the effects of moisture are very noticeable (Table 1). At 27° and 29° C. a large percentage of the nymphs hatched in relative humidities of 32 to 97%, while most of the eggs hatched at 32° and 37° C. in all humidities. A humidity of 97 to 100% favors development of fungous attack, especially at 27°, 29°, and 32° C. The developing embryos were destroyed frequently by fungi a few days before hatching. The fungi were not so troublesome in temperatures of 37° C. or above. The percentage of embryos maturing in the various humidities was somewhat variable in temperatures of 40° C. and above, indicating an inhibiting effect, but was high in most humidities. Only 50% of the eggs hatched in 12% humidity at 27° and none at 47°C., although good hatches occurred in 12% between these temperatures.

It appears that the chorion of *Thermobia* eggs is sufficiently impervious to loss of water in most humidity conditions during the short incubation periods at high temperatures to prevent a lethal effect from loss of water. When the incubation period was much prolonged as occurred at 27° C., the eggs became much wrinkled in 12% humidity and a number of the nymphs had difficulty or failed to emerge from the egg. At times the fully matured embryos could be observed moving in the egg several days after the normal period for hatching had passed, and were apparently unable to break the chorion.

Another evidence showing the effects of the environmental conditions on incubation is the relative size and vigor of newly hatched nymphs. Those hatching at 37°C. and 76 to 85% humidity were plump and vigorous. Specimens hatched in 12 and 32% humidity at 32°, 29°, and 27° C., especially in the latter, were small and weak, but frequently recovered if exposed in favorable environments. None of the nymphs completed the first instar that hatched at 24° C. The same was true of many of the nymphs hatched in all humidities, but especially the dry environments at 42°, 44°, and 47° C. Many of the embryos died after becoming well developed in all humidities at 27° and 42° to 47° C., and in 100% humidity at 29° and 32° C. A number of the nymphs died in all humidities during the process of hatching at 42°, 44°, and 47° C. Many nymphs had the abdomen remaining in the egg chorion in all humidities at 27° and 42°C. and above, and the 12% and 32% humidities at 32°, 37°, and 40° C. Frequently the nymphs did not free themselves from the egg chorion until the first molt.

Apparently the optimum temperature and moisture environment for incubation of the eggs is near 37°C. and 76% to 85% relative humidity. Reference to Table 2 brings this out more clearly regarding temperature. The incubation period was shortest at 44°, but the highest percentage of eggs hatching was at 37°C. The nymphs hatched at 37°C. with favorable moisture conditions were strong and plump, while many were weak at the higher temperatures.

Threshold of Development. The threshold of development was further

determined by plotting the reciprocal of the time-temperature curve (Fig. 1). This curve crosses the base line at 24°C. This indicates that the lowest temperature at which a high percentage of normal nymphs could be expected to hatch would be near 25°C. This is in agreement with experimental data (Tables 2, 3). Apparently the straight line portion of the curve extends from about 28° to 40°C. An examination of the (x-n)y values (Table 2) indicates that 27° and 42° to 47°C. are beyond the straight line portion of the curve. The average daily development at 32°C. appears to be nearer 4.9% than 4.7% as found.

Eggs can be exposed at temperatures below the threshold of development for as much as 6 weeks and still hatch, if placed later in favorable environments (Table 3). The nymphs from such eggs apparently are normal. The effects of moisture are not evident at such low temperature conditions, as eggs hatched that had been exposed in relative humidities ranging from 12 to 100%. The data from several lots of eggs are combined in the table. Since some of the eggs in all lots hatched, it appears that all or most of the embryos, if under favorable conditions, were capable of normal development. Nymphs hatched from about one-third of these eggs following exposures in favorable environments. Fourteen of the eggs were held at or below the threshold temperature for 49 days and still five of them hatched. Longer exposures at low temperatures killed all the embryos. Apparently a slight amount of development occurred at low temperatures as a number of the embryos showed a shorter incubation period after exposure at 37° than with continuous exposure at 37°C. A very evident embryonic development occurs at 24°C. although few eggs hatched (Table 2).

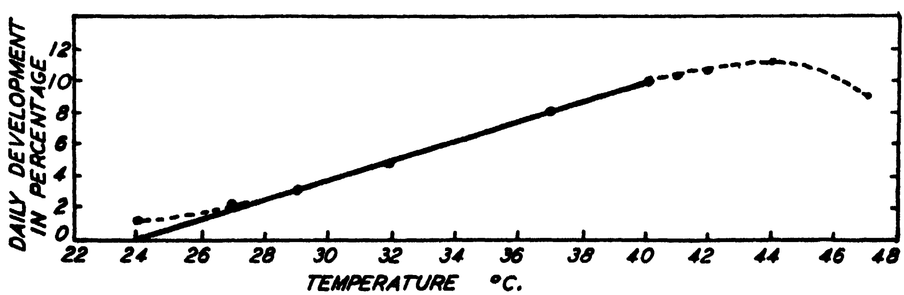

FIG. 1. The threshold of development for eggs of *Thermobia* when exposed at various temperatures and in various humidities.

NYMPHAL STAGE

Description. The newly hatched nymphs are about 2 mm. long, omitting the appendages. They are white, opaque, and free from scales or the ventral abdominal styli. The first instar is more plump and sluggish than later instars. The tip of the abdomen following the first molt is more pointed, the antennae and caudal filaments are greatly increased in length, and the body wall is shiny and tinged with yellow in contrast with the milky white and

opaque appearance of the newly hatched nymphs. The ventral abdominal styli are absent. The body length following the first molt is only slightly increased.

TABLE 3. THE EFFECTS OF LOW TEMPERATURE ON EMBRYONIC DEVELOPMENT OF *Thermobia*.

Number of days at low temperature. °C.	Number of days at high Temperature. °C.	Number of eggs	Number hatched
19° to 22°	*32°*		
34	. .	2	0
84	.	1	0
19° to 22°	*37°*		
8–10	15	3	2
13–16	8–12	18	5
17–20	10–14	8	3
21–24	12–14	10	3
28–31	13–15	4	2
34	.	4	0
39–42	15	5	1
19° to 24°	*37°*		
44–47	7–9	9	4
49–51	9	14	5
58		1	0
66	.	1	0
73		1	0
84	. .	1	0
22° to 26°	32°		
60+	.	39	1
60	8	5	2
22° to 26°	*37°*		
41	8	5	2
60	8	15	4

Early Instars. The nymphs are clothed with scales in the fourth and following instars, except when the scales are rubbed off (Sweetman, 1934). Preceding the third ecdysis for a few hours the scales on the new cuticle can be seen through the old cuticle. This was observed by Adams (1933b) also. The number of days spent in the early instars at 37°C. by 6 nymphs is given in Table 4. One day or less is spent in the first instar, about 4 in the second, about 6 in the third and fourth, approximately 8 days in the fifth to the eleventh, with the period gradually increasing to about 12 to 13 days in later instars. The number of instars depends entirely on the length of the life of the individual. Many pass through from 45 to 60 instars before death. This phenomenon is being reported in more detail in a separate paper (Sweetman & Whittemore, 1937).

The first pair of ventral abdominal styli appears at the fourth molt (fifth instar). The second pair of ventral abdominal styli usually appears on attaining the seventh or eighth instar. The males (see adults) do not ordinarily acquire the third pair of ventral abdominal styli as do the females, which usually acquire this pair in the tenth instar. The number of segments

of the antennal and caudal appendages increased rapidly during the first few instars, but no accurate count was made.

No distinctive sex characters were observed on living specimens before the eighth instar, at which time the posterior abdominal sternites begin showing the notched appearance which lengthens into a definite slit by the time the ovipositor appears. About 10 instars are passed at 37°C. before the ovipositor is visible from a dorsal view.

TABLE 4. THE EARLY INSTARS OF NYMPHS OF *Thermobia* AT 37°C. AND IN RELATIVE HUMIDITY OF 75 AND 84%.

Sex	Instars—Days in Each									
	1	2	3	4	5	6	7	8	9	10
♂.. .	1	4	6	6	6	7	7	8	8	9
♂ .	1	4	7	8	12	7	6	6	9	10
♀... .	1	4	6	6	7	10	9	10	11	
♀ .	1	4	6	6	6	7	6	8	6	9
♀ . ..	1	4	6	6	8	7	7	7	7	7
♀ . .	1	4	6	6	8	7	8		(16)	10

It greatly facilitated the ease of determining the time of molting to amputate one or more of the antennae, cerci, or the caudal filament. Appendages were regenerated after repeated amputations of the same appendage throughout the life of the insects (Sweetman, 1934). Occasionally more than one molt was necessary before normal appendages developed. This frequently was manifested by the beaded appearance of the terminal segments of an appendage during the interval of regeneration.

The young nymphs have a habit of feigning death in the early instars. This habit is discontinued gradually and is seldom exhibited after nymphs become about one-third grown. The color pattern is approximately the same in nymphs and adults, although more definite in the latter. The pigment is in the scales and the pattern is destroyed if the scales are removed. In moist environments, however, the scales may become more deeply pigmented and the light and dark areas of the pattern tend to blend together.

Responses to Temperature and Moisture. Newly hatched nymphs were exposed to a wide range of experimental conditions. The environments varied from 22° to 47°C. and 12 to 100% relative humidity (Fig. 2, Table 5).

None of the nymphs matured in environments below 27° and only a few at 27°C. The greatest length of life at 22°C. was 47 days, showing that this temperature is much too low for normal development. The length of life at 27°C. was much greater. Twelve nymphs lived from 100 to 200 days and 11 from 201 to 294 days, but apparently none of these were mature when death occurred. Five nymphs, 7% of the total, reached maturity at 27°C. Forty-three per cent of the nymphs matured at 32°C. Sixty-six per cent of the nymphs matured at 37°C., but higher temperatures were less favorable. A sharp reduction in the percentage maturing resulted at tem-

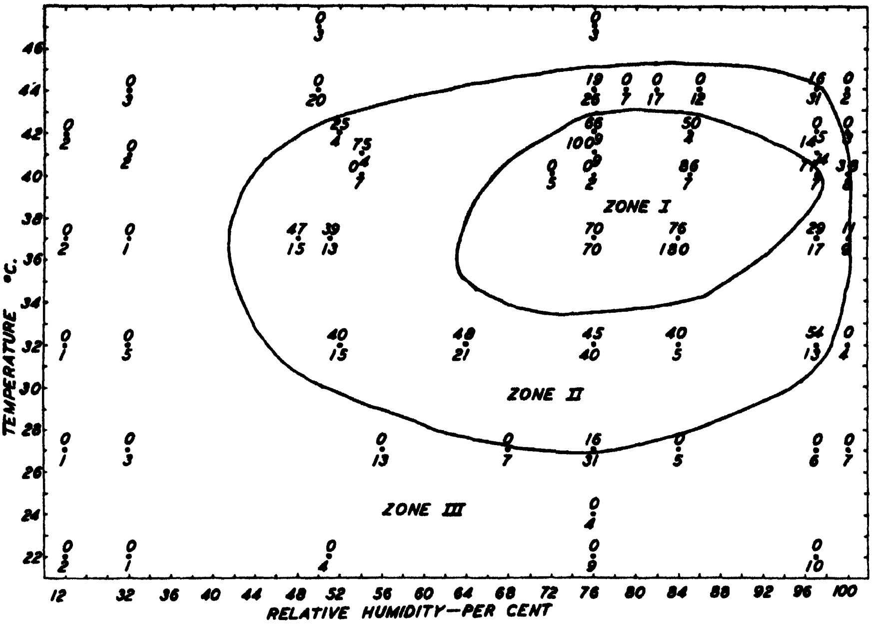

FIG. 2. The percentage of nymphs of *Thermobia* that matured at various temperatures and in various humidities. Figures above dots indicate percentage that matured; those below dots, number of nymphs exposed.

peratures between 42° and 44°C., only 9% completing development at the latter. All of the nymphs died in a few days at 47°C., mostly during the first few days after exposure. The first few instars seem to constitute a very critical period for the nymphs and many hatch that apparently are not capable of maturation even in favorable environments.

Fifteen nymphs (not shown in Fig. 2, Table 5) were exposed to approximate temperatures of 41°C. for about 3 weeks, followed by 44°C. until

TABLE 5. THE PERCENTAGE OF NYMPHS OF *Thermobia* WHICH MATURED AT VARIOUS TEMPERATURES AND IN VARIOUS HUMIDITIES.

Temp. °C.	Percentage Matured in a Humidity of						Total. %
	12-32 %	48-56 %	64-68 %	72-79 %	82-86 %	97-100 %	
22	0	0	..	0	..	0	0
27	0	0	0	16	0	0	7
32	0	40	48	45	40	41	43
37	0	43	..	70	76	23	66
40	0	0	..	0	86	53	40
41	0	75	..	100	..	14	48
42	0	25	..	66	50	0	33
44	0	0	..	15	0	15	9
47	0	0	..	0	..	..	0
Total %	0	22	36	44	64	21	

death or maturation took place. The relative humidities were 54%, 76%, and 96%. Maturation occurred in each environment; 53% of the nymphs matured. This is a much higher percentage of maturation than occurred when nymphs were exposed continuously at 44°C. This indicates that the young nymphs can tolerate 41° much more readily than 44°C.

None of the nymphs matured in relative humidities of 12% and 32% at any temperature (Fig. 2, Table 5). Newly hatched nymphs may withstand these humidities for a few days. None were exposed between 32% and 48% to 53%, but maturation occurred in the latter environments at temperatures ranging from 32° to 42°C. A large percentage of the nymphs can be reared to maturity in 76% to 85% relative humidity at 37° to 42°, but the number maturing decreases decidedly at 44°C. Relative humidities of 97% to 100% are decidedly unfavorable, the majority of the nymphs failing to reach maturity. Part of this unfavorableness was produced by the dampness of the food and sides of the cages which resulted in the nymphs drowning or adhering to the food. Also, fungi in which the nymphs become entangled attack the food more readily in the high humidities, especially below 37°C. The higher humidities were more favorable than low humidities when the temperatures approached the upper limits of tolerance. No definite effects of moisture, in environments where maturation was completed, on the time required for development was detected.

Zones of temperature and moisture combinations that have approximately equal effects on development are evident. Zone I (Fig. 2) demarks approximately the optimum environments for development, where a large percentage of the nymphs can be reared in a relatively short time. The responses to optimum temperature in favorable moisture conditions is shown more plainly in Table 5. Zone II roughly demarks conditions where 50% or less can be reared to maturity. Zone III shows environments that are so unfavorable that none of the nymphs can be reared to maturity.

The length of the period of development from hatching to maturation definitely shows the response to temperature very strikingly (Table 6). No definite criterion denoting maturation could be detected (Sweetman, 1934). Adams (1933a,b) states that sexual maturity is attained in about 11 to 12 weeks at 37°C. after numerous molts. This study indicates that the usual period from egg to egg is greater, although individuals only 7 to 8 weeks old have reproduced. The criterion used to designate maturation in this study is an arbitrary one and is based on the females only. When the ovipositor became visible from a dorsal view, the animals were considered mature. This, at least, serves to show the relative values for the various environments. An extremely wide variation in the number of days necessary for maturation of the nymphs occurred in most environments. This was true frequently among nymphs from the same lot of eggs and reared in the same cage, where the physical environment and food were uniform.

TABLE 6. THE LENGTH OF THE PERIOD OF DEVELOPMENT OF *Thermobia* NYMPHS FROM HATCHING TO MATURATION AND REPRODUCTION. THE FIGURES FOLLOWED BY *a* INCLUDE A NUMBER OF WHICH THE SEX WAS NOT DETERMINED.

Temp. °C.	Number Matured		Days to Mature Females		Age at First Oviposition	
	♂	♀	Range	Average	Range	Average
22	0	0	... ...	...	...	...
27	2	3	308–430	330	...	...
29	10	10	207–371	247	...	...
32	35a	10	65–197	105	138	138
37	46a	27	32–165	92	60–142	113
40	7a	7	63–124	93	109–191	150
41	8	6	28–60	47	47–64	56
41–44	4	4	33–65	42	...	...
42	7a	2	108–125	117	...	..
44	7a	3	38–41	40	...	..

A very rapid reduction in the days necessary for maturation occurred in environments from 27° to 41°C. The period before reproduction occurred was not so definite, probably because of the small number of females involved, and also because the requirements for fertilization (see adults) were not so well understood when this test was made.

A check of the sources of all nymphs in relation to the possible influence of parentage and environment showed that some individuals matured from eggs from every parent which deposited eggs. Of course this occurred only when the eggs were placed in favorable environments. Nymphs exposed at 22° and 27°C. had hatched at higher temperatures and some detrimental effect may have resulted by change to the lower temperature.

Effects of Low Temperature. Several groups of nymphs from one-fifth to fully developed were collected in the laboratory and exposed suddenly to low temperatures at various times during the winter. A summary of the observations follows:

Active	8° and above
Sluggish	0° to 7°
Inactive	0° and below
Survived	0° to -15.5°
Died	0° to -17°

The results must be considered approximate as the time of exposure and variation in temperature was great. It appears that continued exposures of 0°C. or slightly lower are sufficient to kill the nymphs in 4 weeks or less, although several survived much lower temperatures for a few hours. Specimens exposed to cold frequently showed injuries from the exposures, being partially paralyzed. Recovery, if any, was slow and injury was evident for a week or more.

Solitary and Group Rearing. A number of nymphs were exposed at 32° and 37°C. in a relative humidity of 76% to determine the possible effects of group or solitary confinement. Records of the number living were made

at intervals of about 10 days, when the cages were cleaned and new food added. This assisted in keeping the temperature and moisture environments almost constant throughout the tests. Solitary confinement in these environments appeared to be very unfavorable to maturation. The largest percentage was reared at both temperatures when a number of nymphs were placed in 1 cage. Twenty-seven nymphs matured in 1 cage. The data show that crowding can be rather extreme and still large numbers will mature. However, heavy mortality of newly hatched nymphs frequently occurs in 76% humidity, although it is a suitable condition after the nymphs are 1 month old. This experiment was repeated at 37°C. and in a relative humidity of 84% (Table 7). The jars were opened and cleaning of the cages and addition of new food took place at three-day intervals, because of the development of fungous growth if left undisturbed longer. Detailed records of the nymphs were kept for a period of 3 months. Eighty-five per cent were large enough at that time for the sex to be determined while alive. It is evident that this humidity at 37°C. is far superior for percentages maturing to 76% relative humidity. This suggests that crowding produced an environ-

TABLE 7. THE EFFECTS OF CROWDING ON DEVELOPMENT OF NYMPHS OF *Thermobia* AT 37°C. AND IN 84% RELATIVE HUMIDITY.

Number at start	Number matured	Percentage matured	Age of nymphs that died. Months	Relative sizes
1	1		.	Large
1	0		2 5	
1	0	60	2	..
1	1			Large
1	1			Small
5	5			Large
5	4	93	0 5	1 Small
5	5			2 Small
11	8		.25-2	4 Small
10	4	52	5-1	2 Small
10	5		.25-2	Small
11	5		25-2	3 Small
15	13		1.5-2	Small
15	14	73	1 5	12 Small
15	6		.5-1	3 Small
23	12		.25-1	6 Small
21	19	76	5-1	16 Small
22	18		.25-2	15 Small
20	16		25-2 5	12 Small

ment slightly more favorable in a humidity of 76%. This seemed especially true with the very young stages. However, development (size) was somewhat greater among isolated individuals and small groups than among large groups as indicated in the last column in Table 7. This suggests that about 5 individuals per cage was best, as a high percentage of large individuals was produced in 3 months. In large stock cages where ample space was available

there was a strong tendency for all stages to collect in groups where the temperature and moisture conditions were favorable. This was also true of adults (see next section).

ADULT STAGE

Size. Growth continues long after the arbitrary criterion for maturation used in this work, and long after the first eggs are laid. Females frequently more than doubled in both length and weight after their first oviposition. Large specimens attain a weight of about 40 mg. and a body length of 14 mm. (40 mm., if appendages are included). The rate of growth decreases with older specimens, apparently becoming very slight or stationary with many mature specimens.

Mating. The mating process of the firebrat is different from that of higher insects. Spencer (1930) apparently observed mating, but described it merely as a "love dance". The males are most active during the procedure, which starts with the male and female facing each other. The male approaches the female and repeatedly contacts her antennae with his; then he approaches closer and contacts or senses the head of the female with his mouthparts. The female lowers her head and raises her thorax slightly. Her antennae respond slightly to those of the male. The male may rest for a few seconds or minutes after contacting the antennae or head of the female or may turn and crawl away for one-half to two-thirds of an inch and repeat the movements. The male moves the head fairly rapidly from side to side while going toward or away from the female. Soon the male, while moving toward or away from the female, will curl the tip of the abdomen to one side and upward as far as possible with a quivering motion and turning from one-half to completely around with the abdomen in the air. The head is turned slightly in the same direction as the abdomen while whirling. The whirling is always in the direction in which the abdomen is curled, but the adbomen may be curled to the right or left at different times. The curling of the abdomen and whirling may be repeated several times in succession or may be interspersed with only crawling and contacting the female as described at the beginning. At frequent intervals, the male after contacting the head of the female, turns aside and passes the female contacting her legs as he passes. The female then moves forward for about three-fourths of an inch, slowly moving the head from side to side, then turns directly around and faces the male. The male repeats the actions described above. Following a series of curling and whirling movements, the male while twisting the abdomen from side to side and quivering the antennae, deposits the spermatheca on the surface about one-half inch in front of the female. Then the male goes, somewhat more rapidly than previously, to the female and contacts her head and passes by contacting her legs as previously described to a point about 1 inch beyond the female and comes to rest. He shows no

further interest in the female and in 5 to 10 minutes moves away. The male devotes attention to the female for 20 to 35 minutes before depositing the spermatheca. The female immediately on being touched by the male moves forward as mentioned before, straddles the spermatheca and passes on until certain reproductive structures contact the spermatheca. In less than a minute the female has attached the spermatheca, and then turns around and contacts or tastes the spermatheca with her mouthparts. Within 2 to 3 minutes the female begins biting off and eating bits of the spermatheca at intervals of about 1 minute. Twelve to 50 minutes after attaching the spermatheca, the female consumes the remaining portion of it, and thoroughly cleanses the reproductive structures.

Oviposition. Eggs are deposited in crevices, food, or other available places. A female ready to oviposit moves the tip of the ovipositor from side to side searching for a crevice or soft material while slowly crawling about. Apparently females depend upon contacting their ovipositors with a suitable surface rather than on other senses. Once a suitable place is located the ovipositor is inserted as far as possible before eggs are laid. Apparently the females prefer crevices where the eggs can be hidden. In cages, where no other material was available, the eggs were deposited in the food, or scattered loosely on the bottoms of the cages. Frequently the eggs were flattened or otherwise pressed out of shape by the walls of the cavity surrounding them. Adams (1933a) reported similar observations. This distortion must be quite extreme to fatally injure the developing embryo. Occasionally the resulting nymph from such eggs will be misshaped by having a concavity in the head capsule or other part of the body, which disappears on hatching or after molting.

Oviposition Response to Temperature and Moisture. Adults were exposed for long periods of time in various temperature and moisture conditions to determine the influence of these physical factors on reproduction. The environments varied from 22° to 52°C. and the relative humidity from 12% to 100%.

The oviposition records of 215 females which were exposed in the various environments are shown in Figure 3. Results show definite limitations of temperature and moisture in so far as oviposition is concerned. Eggs were developed and laid at 4 different temperatures, 32°, 37°, 40°, and 41°C. Captured females, however, at times oviposited a few days after exposure to temperatures that were unfavorable for development of eggs. This occurred at temperatures ranging from 22° to 42°C. inclusive. No oviposition whatever took place in temperatures above 42°C. A few mature females were exposed at 22° and 27°C. continuously until death. They lived for long periods of time, but no reproduction occurred. A number of males and females were reared and maintained at 27°, 29°, and 32°C. None reproduced at 27° and 29°C. and only a few at 32°C.

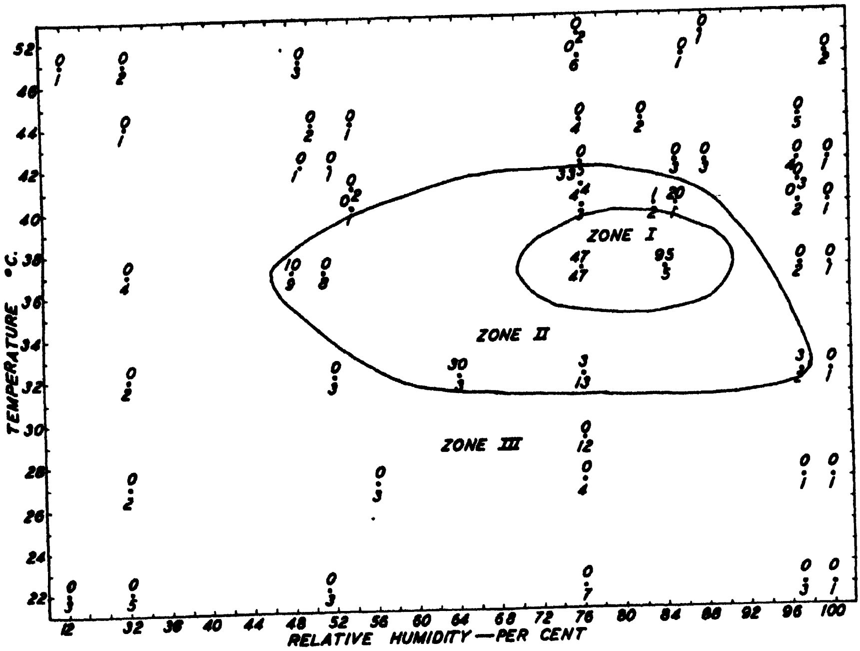

FIG. 3. The oviposition response of *Thermobia* when exposed at various temperatures and in various humidities. Figures above dots indicate average number of eggs per female; those below dots the number of females.

Deposition of eggs occurred in relative humidities ranging from 48% to 97%. A humidity of 84% with favorable temperatures was superior to that of any tested and appears to be near the optimum for egg production (Fig. 3, Table 8). The only moisture condition in which females were exposed at all temperatures used in the tests was 76% (Table 8). Stock cages containing a number of individuals in 76% humidity at 37°C. have consistently yielded large numbers of eggs. When additional males were added to cages that contained non-ovipositing females in favorable environments, oviposition then frequently took place in from 2 to 4 weeks (see fertilization).

Three zones (I, II, & III) showing oviposition response to temperature and moisture can be roughly demarked. Zone I shows the approximate limits of the most favorable region for reproduction. Apparently the optimum temperature and moisture environment for reproduction is near 37°C. and 84% relative humidity. Zone II demarks a region where reproduction occurs and the species could maintain itself, although it would not likely become abundant in such environments. None or very little reproduction will occur in Zone III, and the firebrat could not maintain itself if exposed in such environments continuously.

A few females had reached the maturation stage when 1 month old in

environments at 37° to 41°C. These females began ovipositing when 7 to 8 weeks old. Three females that matured at 27°C. reached maturation when 308, 353, and 430 days old. All were reared in the same cage. This temperature is very near the minimum at which maturation occurs. Incubation (Table 1) and development to the adult stage (Table 6) take place in about 1 year at this temperature. Reproduction, however, does not occur. It has been assumed generally that the life cycle of *Thermobia domestica* requires 2 to 3 years for completion of development. Apparently there is no basis for this general assumption.

TABLE 8. THE OVIPOSITION RECORDS OF *Thermobia* EXPOSED AT VARIOUS TEMPERATURES IN A CONSTANT RELATIVE HUMIDITY OF 76%.

Temp. °C.	Numer of ♀♀	Number of Eggs		
		Lots	Number	Average per ♀
22	7	0	0	0
27	4	0	0	0
29	12	0	0	0
32	13	3	44	6
37	22	57	1094	50
37	25		1118	45
40	3	1	12	4
41	4	6	130	33
42	5	0	0	0
44	4	0	0	0
47	6	0	0	0
52	2	0	0	0

Detailed records of reared females that were kept in favorable conditions and continuously with males show that oviposition may occur when females are 1.5 to 4.5 months old at 32° to 41°C. (Table 6). The youngest female to deposit eggs was reared at 41°C. and 76% humidity. Oviposition took place when this individual was 47 days old.

The individual oviposition records of a number of females that laid eggs are shown in Table 9. The stock either was collected or reared from eggs. The captured females were mature or nearly so when first exposed to the experimental conditions and perhaps had laid a number of eggs preceding capture. There was much variability among the different females that reproduced, both as to the number of lots of eggs and the total number of eggs laid. The variation was from 1 to 195 eggs, with an average of about 50 eggs per female. The greatest number of eggs laid was by a reared individual. During 3 summer months this female was kept at room temperature. A total of 195 eggs in 6 lots was oviposited during its life of 404 days. The first lot containing 32 eggs was laid when the female was 77 days old and the last lot of 35 eggs when 358 days old. One lot, the fourth, contained 45 eggs.

A series of females was tested to determine if a greater number of eggs was laid if exposed singly or in groups (Table 10). A wide variation occurred

TABLE 9. THE NUMBER OF EGGS LAID BY OVIPOSITING FEMALES OF *Thermobia* AT VARIOUS TEMPERATURES AND IN VARIOUS HUMIDITIES.

Temp. °C.	Relative humidity	Number ♀	Number of Eggs: Lots	Number of Eggs: Totals	Reared or captured
32	64	1	6	90	R
32	76	1	2	32	C
32	76	1	1	12	R
32	76	1	1	3	C
32	97	1	1	6	C
37	48	1	4	52	R
37	48	1	4	42	C
37	51	1	1	1	C
37	76	1	1	11	R
37	76	1	6	195	R
37	76	1	3	28	R
37	76	1	1	32	C
37	76	1	1	32	C
37	76	1	3	61	C
37	76	1	3	63	C
37	76	1	3	41	C
37	76	1	2	21	C
37	76	1	6	183	C
37	76	1	7	81	R
37	76	1	1	13	R
37	76	1	5	75	R
37	76	1	2	25	R
37	76	1	1	31	R
37	76	1	2	33	R
37	76	1	12	169	R
37	76	5	..	127	R
37	76	5	..	277	R
37	76	5		191	R
37	76	5	..	287	R
37	76	5	.	236	R
37	84	3	..	365	R
37	84	1	11	108	R
40	76	1	1	12	C
40	83	1	1	3	C
40	85	1	1	20	R
41	76	1	3	67	R

among both individual and group cages, although the average was greater among the group cages. However, the average number of eggs per female is quite similar to that shown in Table 9. Since females can be fertilized only when stimulated to attach the spermatheca, it appears that if several males are available, fertilization will likely occur when the female is in the right physiological state.

A few adults were exposed to daily alternated temperatures in the order of 32°-27°, 37°-32°, 37°-40°, 37°-42°, and 37°-44°C. for 5 to 7 months, unless death occurred sooner. The insects were exposed for 16 hours at the first and 8 hours at the second temperature listed in the alternation. The females exposed at 37°C. in the alternation were in environments suitable for reproduction. No evidence of a stimulating effect on oviposition was apparent.

Behavior Response to Temperature and Moisture. Twenty-five adults (numerous nymphs and adults were added from time to time) were placed for about 18 months in a heated chamber about 3 feet long having a gradient in temperature from about 60° at one end to 22°C. at the other. These specimens had been exposed previously to various temperature and moisture conditions. The relative humidity was maintained at approximately 76%. The insects tended to congregate in a region having a temperature of 35° to 42°C. Occasional excursions were made to the warm end to as high as 50°, while frequent excursions were made to the cool end of the chamber. Occasionally 2 or 3 individuals would come to rest in the cool region for some time. Eggs were deposited in food in the warm region near 38°C. After an exposure in this chamber for several weeks a secondary place of

TABLE 10. THE EFFECTS OF NUMBERS OF FEMALES OF *Thermobia* PER CAGE ON TOTAL REPRODUCTIVE RATE.

Number of ♀♀	Number of ♂♂	First reproduction after exposure. Days	Number of Eggs		Averages	
			Lots	Number	Per cage	Total
1	4	18	7	81	81	43
1	4	18	1	13	13	
1	4	41	5	75	75	
1	4	18	2	25	25	
1	4	18	3	31	31	
1	4	18	2	33	33	
5	4	18		127	25	53
5	4	18		277	55	
5	4	18		191	38	
5	4	26		287	57	
5	4	8		236	47	
3	6	11		365	122	

congregation was observed. This was near one of the sources of moisture where the temperature was about 24°C., thus showing a definite reaction to moisture. Usually less than one-fourth of the total number congregated in this secondary region at any one time.

Longevity. Further evidence of the effect of the various temperature and moisture conditions is more clearly shown by considering the length of life of individuals in the various conditions. The results given in Table 11 show this very strikingly. The record of the longest living individual only is shown for each environment. Frequently other individuals lived almost as long. The captured individuals were of unknown ages when first exposed, but were mature or nearly so at that time. A humidity of 12% to 32% was very injurious and killed the insects in a few days. As one might expect the effect was lessened with a reduction in temperature. Usually a noticeable shriveling of the insects could be detected several days preceding death in temperature environments below 44°C. These shriveled individuals readily recovered when placed in moist environments, except in

advanced cases of desiccation. When placed in the vicinity of water none of the desiccated insects responded to it, but some imbibed the liquid freely when placed in contact with it. A humidity of 48% to 56% falls near the border of the favorable zone (Fig. 3). Here again the greatest length of life occurred below 40°C., but the great increase in days lived over that in lower humidities shows that these conditions can be tolerated for long periods. The greatest number of long-lived individuals was in humidities ranging from 64% to 85%. Several individuals lived over 2 years, some being of unknown age but mature when captured. Apparently temperatures of

TABLE 11. THE GREATEST LENGTH OF LIFE IN DAYS OF *Thermobia* AT VARIOUS TEMPERATURES AND IN CONSTANT HUMIDITIES. THE LETTER *e* INDICATES NYMPHS REARED FROM EGGS, ALL OTHERS WERE CAPTURED; *a* INDICATES NEXT LONGEST LIVING INDIVIDUAL LIVED 385 DAYS; + INDICATES THAT EXPOSURE IN THAT PARTICULAR ENVIRONMENT WAS DISCONTINUED.

Temp. °C.	Length of Life in a Humidity of			
	12-32 %	48-56 %	64-85 %	97-100 %
22	30	300	418	316
27	19	682	757e	599+
29	.	.	552e	
32	14	260	1033e	239e
37	10	675a	661	109
40	10	87	218+e	209e
42	4	253+e	239e	228
44	5	247e	359e	103e
47	2	12	18	11
52	..	.16	.16	.16

27° to 37°C. with this humidity range were far superior to other conditions for length of life. High humidities, 97% to 100%, were unfavorable, especially at higher temperatures. Such conditions can be tolerated, however, and reproduction occurred at times. Within the range of environments where mature specimens could be reared from the egg (32° to 44°C. and 48% to 100%) a large majority of the long-lived individuals were reared specimens.

Extreme High Temperatures. The results from the exposure of a number of nymphs and adults to high temperatures are given in Tables 12 and 13. When the injury from high temperature is sufficient to incapacitate the specimens so that they cannot crawl (Table 12) recovery does not occur. Temperatures above 55°C. killed the insects in a few minutes, but between 48° and 55°C. signs of life were visible for some hours after they became incapacitated. The length of the exposures necessary to produce death is shown in Table 13. One individual apparently was not injured after being exposed to 52°C. for 32 hours. This was the only survivor of 65 individuals exposed to temperatures ranging from 48° to 52°C. The maximum temperature that could be withstood by most individuals for a few days or more is 47°C. Sixty-seven nymphs and adults were exposed at this temperature. Fifty-one were killed in 19 days or less, while 16 lived longer periods, one nymph sur-

viving a 47-day exposure. Heat-injured individuals appear partially paralyzed, sometimes for several days before death or after removal from extreme temperature.

TABLE 12. THE LENGTH OF LIFE OF *Thermobia* ADULTS AT EXTREME HIGH TEMPERATURES. DATA RECORDED BY HAROLD MORLAND, M. S. C., 1935.

Temp. °C.	Number exposed	Time to incapacitate. Minutes
69.4	1	2
67 5	1	2
66.1	1	2
63.9	1	2
62.8	1	2
60 6	1	2
59.4	1	3
57.7	1	3
55.3	1	5
54.2	1	12
52 5	4	15 6
5u.3	3	33
48.1	2	167

TABLE 13. THE LENGTH OF LIFE OF *Thermobia* AT EXTREME HIGH TEMPERATURES.

Temp. °C.	Number exposed	Adults or nymphs	Dead at end of	Alive after
52	51	AN	1.5–36 hours	.
52	1	N		32 hours
50	10	AN	2 5–14 hours	
49.	1	A	1–4 hours	
48 5	1	A	23–28 hours	
48	1	A	6 hours	
47	8	AN	.25– 5 days	.
47	37	AN	.2 days	
47	5	A	6–12 days	
47	1	A	19 days	
47	1	A	25 days	
47.	13	A		17–21 days
47	1	N	. .	29 days
47.	1	N	.	47 days

Fertilization. It has been observed that unfertilized females never reproduce. Frequently females reproduce in 1 to 2 weeks after being placed with the males. True copulation does not occur (see mating). The results from a number of females kept separate from males for definite periods are given in Table 14. Some of the females were kept with males for short periods of time only. One lot of 5 sisters (Nos. 1 to 5) were reared together. The ovipositors were visible on all of them when 47 days old. Two of these females were placed with males at that time. One of these laid eggs 13 days later. The other female oviposited months later after being placed with other males. Two of the sisters were placed with males 16 and 77 days after maturation, the latter to several males. Neither of these laid eggs. The fifth sister was not placed with males and died when 179 days old without opivositing. Since only the

two females that were placed with males at maturity reproduced, it suggested that fertilization near the time of maturation might be necessary. In order to test this hypothesis a new series (Nos. 1 to 19) was started. These males and females were reared from 3 lots of eggs laid on approximately the same date. The specimens were isolated when 1 month old and reared to maturity separately. The females were allowed to remain with males at different ages and for various periods of time. Nos. 6 to 10 were placed with males for periods of 1 to 4 weeks as soon as their ovipositors were visible. Nos. 11 to 19 were placed with males when approximately 1, 2, 3, and 4 months beyond the maturation stage. Successful fertilization occurred in 33% of the associations with a single male of the same age as a female. Fourteen females were placed with males a second time or from the start of the test with several

TABLE 14. THE RELATIONSHIP BETWEEN TIME OF MATING AND REPRODUCTION OF *Thermobia* WHEN EXPOSED AT 37°C. AND IN 76% RELATIVE HUMIDITY.

Age when mature. Days	Days between maturation and association with males	Days With Males		Number of Eggs Laid		Days with males before ovipositing
		First time	Second time	After first males	After second males	
47	0	cont.	..	22	..	13
47	0	"	..	11		345
47	16	"	..	0	.	.
47	77	"	.	0	.	.
47		..	.	.		
102	0	7	.	0	.	
125	0	7	19	0	10	19
118	0	14	30	0	35	30
115	0	21	42	5	0	21
125	0	28	42	0	0	
118	0	cont.		35	..	235
139	30	"	.	31+	.	29
137	30	"	19	7	22	8
145	60	"	..	17+	..	205
145	60	"	19	0	0	
173	90	"	.	88		25
151	90	"	.	88	..	25
165	120	"		37	..	73
165	120	"	19	0	23	7

males of variable ages. Most of the females laid eggs. It appears that the age of the male and female is not an important factor in successful fertilization. Individuals of the same age do not necessarily succeed in fertilization. The ages of maturation of the females that reproduced were quite varied, suggesting that rate of maturation has no effect on fertilization. Two females were 145 and 118 days old and had been with males for 7 and 8 months respectively before laying eggs. It appears that fertilization can be successful at least from the time of maturation to several months after maturation and even throughout life, provided the physiological condition of both sexes is suitable.

A further test of groups of young females associated intermittently with

approximately an equal number of males is shown in Table 15. The females were reared specimens that had not reproduced when the test was started. Each cage contained 5 females at the start and the tests were continued until all had died. Males were added so as to have 3 to 5 in the cages at all times. Egg laying after separation from males occurred once, 9 days after removal. It is evident this female was fertilized before the males were removed. One egg was recovered from the same cage in another instance 22 days after males were removed. The embryo failed to develop, suggesting it was an infertile egg; probably left in the cage when the males were removed. These data clearly demonstrate that fertilization is necessary for reproduction, that fertilization must occur frequently, and that fertilization and reproduction can take place repeatedly throughout the greater part of the mature life. Occasionally females oviposited in the instar preceding death. Frequently females failed to reproduce during or following long association. Usually the

TABLE 15. THE EFFECTS OF INTERMITTENT ASSOCIATION OF FEMALES OF *Thermobia* WITH MALES.

Number of ♀♀	Days with ♂♂	First reproduction after association. Days	Total number of eggs	Days without ♂♂	Number of eggs	Number of ♀♀ left	Days with ♂♂	First reproduction after association. Days	Total number of eggs	Days without ♂♂	Number of eggs	Number of ♀♀ left	Days with ♂♂	First reproduction after association. Days	Total number of eggs
5	51	25	52	69	0	3	53	32	34	49	0	2	Cont.	10	92
5	51	38	33	69	0	5	53	14	58	49	0	2	"		
5	51	21	38	69	1	3	53	22	32	49	22	2	"	20	37+
5	50	17	115	69	0	4	53	14	60	49	0	2	"	19	42

addition of several males to a cage with females increased the number of eggs laid. Careful observation of pairs shows that the two sexes must molt within a few days of each other for successful fertilization to follow (Table 16). The results show that with 16 lots of eggs from 2 females, the males molted on or within a period of 3 days before or 5 days after the females. This suggests that the females are capable of or stimulated to attach the spermatheca only during about the first half of each instar. Fertilization must take place for each lot of eggs, and only one lot of eggs is deposited during an instar.

Ventral Abdominal Styli. It was shown in Table 4 that the ventral abdominal styli usually appeared in the fifth to tenth instars. The females typically have 3 pairs and this can be used as a partial means of determining the sexes. An occasional female may have only 2 pairs of styli. The males typically have 2 pairs, but a third pair or one stylus of the third pair frequently develops. Apparently the number of styli other than the typical, does not indicate intersexes as reproduction of such individuals was normal. A more detailed report regarding the development of the styli is being published elsewhere (Sweetman & Whittemore, 1937).

TABLE 16. THE RELATIONSHIP OF TIME OF MOLTING OF THE SEXES OF *Thermobia* AND REPRODUCTION.

Instar of female	Number of eggs laid	♀ oviposited after molt. Days	♂ molted before or after ♀. Days
14	2	5	3b
16	13	4	2b
17	22	5	0
20	24	3	1a
21	19	5	3a
22	16	7	0
26	28	5	1b
27	1	9	0
29	25	5	4a
30	7	6	
31	11	7	
35	1	10	0
17	15		
18	15		
19	1	5	2a
20	12	6	
21	14	8	4a
22	9	4	5a
23	13	5	
24	6		
29	6	8	2b
31	16	8	0
33	1	10	0

CONCLUSIONS

The firebrat is a common household pest that is a general scavenger and feeds on many carbohydrate and protein containing foods as well as starchy paper and cloth. Since it tends to remain hidden during the day, much of its damage to food remains unnoticed or is discovered only after much feeding has occurred.

The firebrat can be reared and bred continuously in cages, provided the physical environment and food are suitable. The insect requires a high temperature and relative humidity for development. The general optimum physical environment for all stages is near 37°C. and 84% relatively humidity. In such environments with ample food the firebrat has the potential to become very abundant and consequently capable of producing considerable damage to materials that the insect will eat.

Eggs. Hatching of the eggs occurs in environments ranging from 24° to 47°C. and moisture ranges of 12% to 100% humidity. The eggs can withstand considerable periods of exposure below 24°C. and still hatch if placed in favorable environments. The optimum condition for incubation of the eggs is near 37°C. and 84% humidity. Light at ordinary exposures has no effect on hatching of the eggs. The incubation period ranges from about 75 days at 24° to about 9 to 10 days at 47°C. The incubation period under optimum conditions requires 12 to 13 days.

Nymphs. The nymphs will develop to maturity in environments ranging from 27° to 44°C. and moisture ranges of 48% to 100% humidity. The optimum physical conditions for maturation of the nymphs is near 38°C. and 84% humidity. Maturation occurs in 2 to 4 months in optimum environments. The nymphs are readily killed by temperatures below 0° and above 44°C. No definite reaction to ordinary light occurs.

Adults. The adults develop eggs and oviposit at temperatures ranging from 32° to 41°C. and moisture ranging from 48% to 97% humidity. The optimum conditions for reproduction are near 37°C. and 84% humidity. The eggs are laid in crevices or hidden in food or debris. Only a few individuals can withstand temperatures above 47° C. for more than a few days. The average number of eggs per female is near 50, although wide variations in the number deposited by individual females occur. The length of life in favorable environments is about 2 to 2.5 years at 32° and about 1 to 1.5 years at 37°C. Oviposition at 37°C. occurs from about an age of 2 months to the end of life. Only 1 lot of eggs is laid during an instar and fertilization must precede each oviposition.

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SEASONAL VARIATIONS IN ABUNDANCE OF CERTAIN ESTUARINE AND MARINE FISHES IN LOUISIANA, WITH PARTICULAR REFERENCE TO LIFE HISTORIES

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CONTENTS

SEASONAL VARIATIONS IN ABUNDANCE OF CERTAIN ESTUARINE AND MARINE FISHES IN LOUISIANA, WITH PARTICULAR REFERENCE TO LIFE HISTORIES[1]

INTRODUCTION

At the inception of the Shrimp Investigations of the United States Bureau of Fisheries, which were begun in Louisiana in 1931, in cooperation with the Louisiana Department of Conservation, it was apparent that data on other animals of this area could be collected along with those on shrimps. Such material is of value for its own sake and as a supplement to the primary investigation. This paper treats of some of the data on fishes collected in trawls from October, 1931, to March, 1934, covering a period of two and a half years.

The writer wishes to acknowledge his indebtedness to all people connected with the Shrimp Investigations in Louisiana, many of whom have assisted in innumerable ways.

Aims

The objects of this work were:

1. To study the destruction of fish by trawls with the view of learning something of the number, species and relative importance of fishes destroyed in Louisiana by shrimp fishermen, who take about ninety per cent of their catch in trawls. This problem has been considered by Gunter (1936).

2. To study the natural history of such fishes as would be taken in the trawls by:

a—Analyses based on abundance, with which the present paper is chiefly concerned. b—The study of relative numbers of the various species (Gunter, 1938). c—Studies of the environment, as evidenced by hydrographic data.

COLLECTION OF DATA

The objects of the work can be more clearly understood if some of the characteristics of the area studied are known. The following is a brief account.

The territory selected for intensive study was Barataria Bay and the adjacent waters of the Gulf of Mexico. The choice of this area was determined by its accessibility and the extensive shrimp industry located there. Barataria Bay is shallow (2-12 feet deep), soft-bottomed, has several islets, and is located in the heart of the Louisiana coastal marsh about forty miles northwest of the mouth of the Mississippi River. It is connected with the Gulf of

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Mexico by a number of narrow passes. The depth of gulf waters increases very gradually, so that twelve miles from shore it is only ten to twelve fathoms.

The method of collecting data has been stated by Weymouth, Lindner and Anderson (1933), and only the essentials will be given here. Five stations were selected and visited on an average of twice each month. These ranged from the brackish headwaters of Barataria Bay to six miles out in the open gulf. The map (Fig. 1) shows the stations marked in heavy lines. The

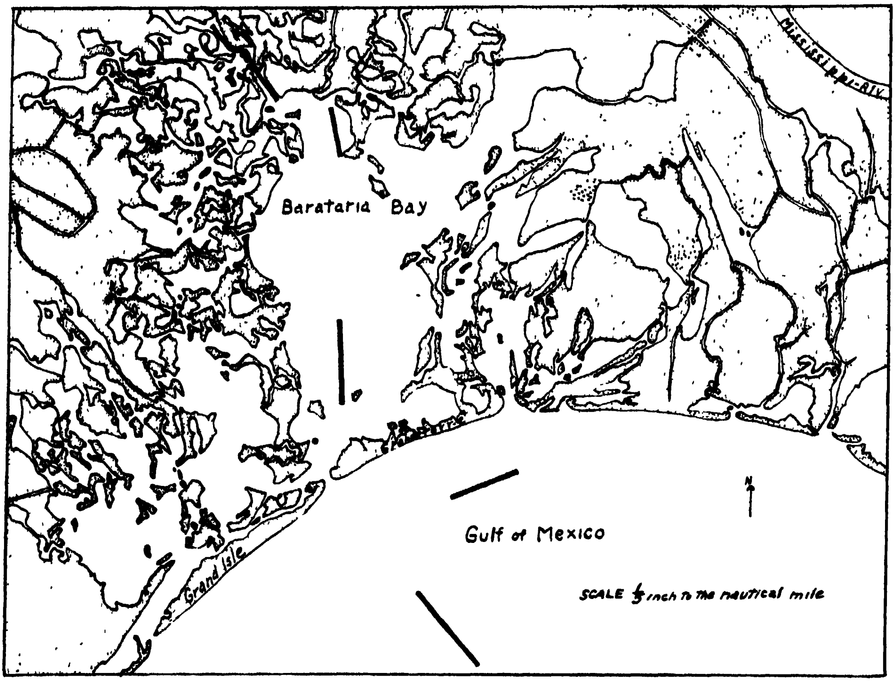

FIGURE 1.
Map of Barataria Bay and adjacent waters. The stations are marked in heavy lines.

first covers the lower end of Bayou St. Denis. The next one extends from Myrtle Grove Canal to St. Mary's Point. The following station is from Middlebank Light to Independence Island. The first station in the Gulf of Mexico paralleled the beach one mile offshore and extended from Quatre Bayou Pass to another pass called Coup à Belle. The second outside station was from three to six miles southeast of Barataria Pass. Whenever it was deemed worthwhile other hauls were made in various places, but not with the regularity that the five main stations were visited. Data from the places visited irregularly are not given here.

At each place a drag was made with an ordinary otter trawl of thirty-five feet wingspread and a mesh measuring three quarters of an inch square. The

hauls were approximately of one hour's duration. A hydrographic station was made at each drag by Louisiana Department of Conservation officials. The material caught was placed on the aftdeck of the boat and separated into piles according to species. Counts of each species were made and recorded. Notes on the size were made. The present data are almost wholly on abundance as derived from actual counts in trawl hauls.

Occasionally, the trawls would become so full of shrimp or jellyfish in the full period drag that they could not be raised, so it became necessary to cut the length of haul to one-half or one-fourth of the usual time. At other times sharks and porpoises tried viciously to get at fish within the trawl and in so doing cut large holes in the bag. The trawl was sometimes left down only a short while to avoid the actions of these predators. Whenever the time was cut short the numbers of fish were weighted, so that they were made as nearly equivalent to a full time haul as possible. Rarely there were a great many fishes and a limited time to count them, so they were divided into two equal piles and one-half of them counted. This number was then multiplied by two to make it equivalent to a whole haul. Obviously, this is not strictly accurate, but the writer believes that the percentage of error in a large number of fishes is negligible for purposes of this paper.

The advantages of this method of collecting data are: (1) The regular collection of samples was at set stations covering a wide range of conditions from almost fresh to pure sea water, over a period of time which shows seasonal fluctuations at a given station. (2) The otter trawl is especially fit for the catching of slow-moving bottom forms. It is less efficient for catching fast-swimming active fishes, although the young animals of this type are sometimes taken in abundance. Specimens caught ranged in size from post-larval anchovies to a 300-pound spotted whip-ray. Taken all around the otter trawl seems to be as useful in this type of study as any single unit of gear that could be devised. Although it is inefficient in clear water as pointed out by Beebe (1934), the coastal Louisiana waters are generally of high turbidity.

EXPOSITION OF DATA

Tables giving the actual count of specimens taken would fill a large volume. There is not room for them here so another method of presentation is used. All hauls for a given month were thrown together and the total number of every species was divided by the number of hauls. This gave the average number of each species taken per drag for each month. The numbers are given in Tables 1 and 2. The curves were made from these tables. The numbers of hauls are given for every month for both the bay and the gulf in Table 3.

Unfortunately, in some months hauls were not made. Those missing are November and December, 1931; and January, 1932, for the gulf; and March, 1934, for the bay. In February, 1932, no hauls were made.

TABLE 1. AVERAGE NUMBER OF FISHES TAKEN PER HAUL, BY MONTHS, IN BARATARIA BAY

	1931			1932												1933												1934	
	O	N	D	J	F	M	A	M	J	J	A	S	O	N	D	J	F	M	A	M	J	J	A	S	O	N	D	J	F
Achirus lineatus	2.0		6.0					0.5	0.3			8.0	12.8	2.5	0.2	0.1	0.7	0.2	0.2	1.1		0.1		0.2	6.4	2.6	0.3		0.3
Anchoviella epsetus	1.0	11.3	27.7	10.7		77.7	92.6	39.1	15.3	13.0	34.7	2.2	23.7	8.7	76.7	68.1	76.4	30.2	47.7	13.6	1.8	19.5	18.3	3.7	17.4	5.9	19.5	28.6	2.0
Bagre marinus	1.5						0.3	0.4	3.1	2.2	13.1	66.5	4.5	0.5		0.1	0.1	0.2	0.2	1.0	1.0	1.6	9.6	36.2	11.8				71.3
Bairdiella chrysura	4.5	4.0	12.0	74.8		1.0	0.4		0.6	1.0	11.3	0.2	3.9	2.0	0.9	0.4	2.1	0.2	0.3	1.3	0.2	31.8	5.0	0.8	1.8	13.1	3.3	21.1	
Brevoortia patronus	6.0	5.7	15.3	220.5		30.8	30.2	3.9	0.9	0.2	1.4	12.5	4.5	13.8	39.7	39.7	11.3	7.5	11.9	7.7	1.8	5.2	61.3	5.0	31.8	11.1	34.3	102.8	191.0
Caranx hippos										0.2	2.6	0.2											1.6	0.2	0.1	0.1			
Chloroscombrus chrysurus	0.5										1.7	0.2	0.5										0.3		3.9				
Citharichthys spilopterus		2.0	3.3			0.1		0.7	3.2	1.3	8.7	42.5	3.7	1.8	0.6			0.5	0.2	2.8			0.4		33.9	4.9	1.3		1.3
Cynoscion arenarius	4.5	11.0	2.0	8.0		1.3	1.3	17.5	57.6	13.7	114.9	21.2	50.6	7.2	4.1	0.3	1.1	1.8	4.5	43.7	24.0	44.5	39.3	42.3	15.7	15.6	12.0	1.8	6.7
Cynoscion nebulosus			4.0	10.2		3.4	0.6	0.3	0.3	0.7	0.1	1.0	1.8	7.7	7.7	33.7	12.7	1.5	1.1	1.3	0.5	0.1	0.3	0.2	0.9	1.6	1.0	6.8	8.7
Cynoscion nothus															1.7	0.1				2.9									
Dasyatis sabina				0.7					0.2		0.1	0.7	0.2	0.7		0.1	1.5		0.1		1.0	0.4	0.1	0.2	0.4	0.1	0.2		
Etropus crossotus		2.0	4.0	2.5		3.6		0.2	0.9	0.2	3.4	86.0	5.6	7.2			2.9	1.2	0.2	0.7		1.9	0.9	1.0	10.0	2.0	0.2		
Galeichthys felis	1.5	18.0	35.7	0.5		7.3	5.0	11.1	18.7	7.0	28.3	66.8	34.8	35.3	8.8	0.3	18.3	17.9	14.1	21.0	10.7	8.5	8.9	12.8	34.1	5.6	4.2	1.5	13.3
Larimus fasciatus								0.1					0.1	0.3	0.1														
Leiostomus xanthurus	1.5	0.3	0.7	4.5		1.4		6.4	15.1	7.3	7.7	2.3	4.8	0.7	0.1		0.1	0.2	1.1	25.8	4.0	12.2	89.9	7.2	9.0	12.1	1.7	42.3	22.7
Menticirrhus americanus			0.3			0.3	0.3	0.5	0.3	0.3	0.4	3.3	4.0	1.2	0.1		0.6	0.2		3.3	0.8	0.5		0.7	1.0	1.6		0.2	0.3
Micropogon undulatus	4.5	0.3	5.7	27.7		46.3	34.1	197.5	344.8	163.2	136.6	125.0	5.5	0.8	12.2	14.9	77.8	241.6	495.0	813.7	20.2	217.2	159.1	63.3	26.6	3.7	0.3	5.5	79.7
Paralichthys lethostigmus			0.7	3.0		1.6	1.1	1.4	2.1	0.7	1.0	1.3	0.8	0.3	0.2			0.3	0.6	2.3	2.8	1.5	2.6	0.8	1.7	0.3		0.3	0.3
Polynemus octonemus								2.6	6.7	4.0	15.3	14.7	1.8						11.1	59.9	1.3	72.1	29.6	7.3	1.7				
Poronotus triacanthus						1.0	0.9	0.2		0.2		0.3	1.1		0.2		0.2	13.0	8.4	15.1	8.2	1.2	1.3					0.2	1.0
Selene vomer																													
Signalosa atchafalayae			0.7	3.5		0.6	0.6	0.1	0.2	0.3	0.1	3.7	2.5	0.5	10.3	2.0	2.8	0.5		0.1		1.5	2.0	1.2	3.0	1.0		3.2	5.0
Stellifer lanceolatus			5.3						3.3		0.3	97.8	5.9	0.8		0.4	0.1		0.4	1.3	0.7	51.1	0.6	6.0	42.3	0.4			
Symphurus plagiusa		0.3	1.0	0.3			0.1	0.1			1.3	25.2	2.1	1.0	0.1	0.4	0.1		0.4	1.3	0.7	0.1		0.7	3.3	0.6		0.7	
Trichiurus lepturus	2.0	0.7	0.7	0.3		0.2	2.6	1.1	4.0	1.2	0.7	2.8	3.5	0.2	0.1	0.3	0.2	1.5	0.5	12.2	1.8	29.4	34.9	35.0	9.6	5.9	3.0	6.3	2.0
Trinectes maculatus	0.5	1.3	20.7	0.3		2.0	0.7	2.0	1.9	0.5	4.3	28.7	8.6	3.8	0.3	2.6	4.7	19.5	19.8	35.0	0.2	6.4	5.3	1.5	13.4	3.0	0.7	0.7	1.7
Urophycis floridanus						0.1	0.5								0.4	1.4	3.2	1.6	0.6	0.3									
Vomer setapinnis	41.5	0.7	0.3						0.1	2.8	9.1	18.0	6.1	0.2					0.1			0.9	8.0	26.3	65.6				

TABLE 2. AVERAGE NUMBER OF FISHES TAKEN PER HAUL, BY MONTHS, IN THE GULF OF MEXICO

	1931	1932										1933												193		
	O	M	A	M	J	J	A	S	O	N	D	J	F	M	A	M	J	J	A	S	O	N	D	J	F	M
Achirus lineatus	.	0.7	0.6	1.3	2 3	0.2			1.5	2.3			0.8	0.7	0 1	. .		. .	.	.	0 3	0.3	1.0		2.0	. .
Anchoviella epsetus	0.8	39 0	63.0	10 41	39.2	8.5	15.0	8 3	2.4	5 0	20 0	17.4	32.1	7.2	16 8		0.3	36.5	33.1	12.7	15.7	18.7	29.0	48.8	13.5	1.0
Bagre marinus		.			0 5		.		4 5	1 8	4 3	0 3	0.8	1 8	0 9			11.5	21.5	31.3	0.7	2.3	1.0	.	.	.
Bairdiella chrysura		9.0	0.1	2.9	4 5	1.2	1.3		0 5	3 3	3 0	2 4	3 8	0 1	5 5		11.0	4.0	0.5		..	0.7	3.3	0.2		1.0
Brevoortia patronus	0.5	0.7	6 1	0.9	2 8	6.0	1.3		0 8	1 8	1 3	0 7	0 8	1 3	4 0	1 0	4 7	58.0	2 1	3.3	2.7	1.3	3.3	8.0		..
Caranx hippos	0.3					1.2		1 3		1 0			..		0 5			.		.		0.3	.	.		.
Chloroscombrus chrysurus	.							2 5	2 9	2 3	0 3			34 7					0.9		4 0	8 7	0 7			
Citharichthys spilopterus					0 5			2 0	1.8	0.3				2 0				.	0 1		5.3		1.3	0.2	1.5	22.0
Cynoscion arenarius	10.8		3 4	5 7	80 8	71.8	13.7	35 8	28 3	18.8	44 7	1 4	38.6	7 2	25.6	4 0	21 3	.	58 9	36 7	28.0	29 0	79.7	3.2	9.5	3.0
Cynoscion nebulosus		3 7										0.7	0 3								.	.	.			..
Cynoscion nothus			0.1		1 3		111 3		5 3	1.5	11 7	4 0	11 9	9 8	5 3	1 0		43 0	18.4	1.0					0.4	..
Dasyatis sabina							.					0 9		.			0 3						.		0.5	.
Etropus crossotus		3.3	0 1	0 1	0 2	1 0		9 8	1.9	1.5	1 0	9 3	4 0	1 0		1 0	.	21 5	3.1	0 7	0 3	0 7	3.3	1.8	6.0	.
Galeichthys felis	0.8	0.3	4.8	3 3	9 3	7.8	10 7	40 0	12.4	7 0	26 0	29 0	13.3	22 2	6 1		65 7	12 0	10.1	8.7	4 3	9.0	9.7	5.2	7.0	. .
Larimus fasciatus	0.3			0 2	3 2	2 0	9.7	2 3	3 8	0 8	0 3	0 6	0 6					0.5	5.9	.	0.3	1 3	.	1.0	2.0	
Leiostomus xanthurus	0 5			2 6	48.3	75.0	1 7	3.0	0 6	1 3	0 3	1 3			37.9		12.3	10 5	11.9	2.0	0 7	3 3	3.7	116.0	5.5	
Menticirrhus americanus	0 5		2.6	0.3	2 7	1 7		9 0	11 6	3 3	17 0		44.6	34.2	3 9		6.3	8.5	1.2	3 3	0.7	21.0	6.7	5.0	7.0	3.0
Micropogon undulatus	17.5	115 3	3.5	271 6	446 0	451 5	472 0	1728.0	683.1	129 3	55.0	5 0	0 3	1.0	65 1	35 0	696 0	353 5	291.2	47 7	22 3	43.7	329.3	2 4	1.0	70.0
Paralichthys lethostigmus	..	1 7			0 2							0.1				1.0	2.3	0.5				.			1 0	1.0
Polynemus octonemus	5 0			3.7	23 0	21 7	2 7	14 3	7.6						0 8	2 0	9.3	24.0	26 7	1.7	1 0		.		.	.
Poronotus triacanthus	0 3		2 1	0 1	0 2					0 3	3 7	1 0	20 5	49 7	28 5	10 0	26 3	7.0	0.1		.			0 4	0 5	. .
Selene vomer	33 8	1 0	1 1					11 5																		.
Signalosa atchafalayae		1 0	0 4							0 8	1 7	0 6	0 1	0 8	.		1 3		0 1		0 3	0 7		5 4	4.5	.
Stellifer lanceolatus	9 3		1 8	18 2	107.5	106 7	61 7	315 5	135 5	57.3	42 3	18 3	22 9	19.7	28.5	35.0	39 3	222.0	171 0	101.3	50 3	31 3	40 3	2.6	59.5	1 0
Symphurus plagiusa	0.3		0 1	0 5	0 5			13 8	1 4	0.5		4 6	2.6	1 0	0.5	2 0			0 4				2.3		1.0	14.0
Trichiurus lepturus	8 0	9 3	2.4	35 1	56 3	55 7	24.3	30 8	5 8	9 8	39 7	12 7	33 1	17 2	18 9	3.0	2.7	44.0	56 0	28.0	5.0	7.3	25.0	4.6	50.5	6.0
Trinectes maculatus	0 3	1 0	5 0	3.5	6 5	5 5	7 3	52 0	14 9	0 5	3 3	7.3	13.1	28 0	2 4	2 0	1 3	0.5	1.0	0.3	0.7	5 3	6.3	0.6	2.0	1.0
Urophycis floridanus			0.1			.						1.3	2 9	1 5			.				.	.	.		1.0	1.0
Vomer setapinnis	19 3	0 7		0 9	0 2	12 3	4 7	1 5	11 3	3 8	15 3	1.9	1 8	60.7	19 1	.		1.0	45.6	38.3	126.0	11 0	3.0	0 8	5.5	5.0

TABLE 3. NUMBER OF HAULS MADE EACH MONTH AT STATIONS IN BARATARIA BAY AND THE GULF OF MEXICO

Months	1931		1932		1933		1934	
	Bay	Gulf	Bay	Gulf	Bay	Gulf	Bay	Gulf
January...	..		5	0	7	7	6	5
February..			0	0	12	8	3	2
March...... . .	.		9	3	12	8	0	1
April.		.	12	8	11	8	..	.
May..	.		14	10	9	1		
June...... .	.		9	6	6	3		.
July			6	8	10	4		
August	.		7	3	7	8		
September. . .			7	6	6	3		
October	2	4	12	8	7	3		
November ..	3	0	6	4	7	3		..
December .. .	5	0	9	3	6	3	.	.

Curves were drawn for all species caught in sufficient numbers. The tables are used for the discussion of some of the less numerous fishes. Several species were not caught often enough for continuous tables or curves and are excluded. Catch records for the rarer fishes have been given by Gunter (1935). The hauls were divided into inside and outside groups and corresponding tables and curves made. The differences between inside (bay) and outside (gulf) waters are sharp enough to warrant such a division. Each species is treated individually.

SEASONAL VARIATIONS IN ABUNDANCE

Seasonal variations were among the first phenomena of life that man noted. The particular variation under consideration here is one of abundance, and is related to numerous other variations or cycles, such as spawning, migrations, variations of food, the cycles of seasons, and abundances in other animals in a number of known and unknown ways.

One of the first questions that arises is what causes seasonal changes in animal numbers? Why should a fish which seems to be more or less homogeneously distributed over an area suddenly become ten or a hundred times more numerous than before? Most animals have definite seasonal breeding periods within each year. These reproductive cycles bring about annual variations in numbers of the total population. Holding in mind that the method of detection used here is abundance in trawl catches in one locality, it is plain that these peaks may be seemingly caused or made apparent by two things: (1) An influx of young which were hatched and raised in the region, and which have attained size enough to be taken in the trawl (as was indicated above this is not at all large), or (2) A migration of young or old individuals from another locality. The young may be migrating to or from nursery grounds. The older animals may be moving to or from spawning grounds, or on a seasonal migration brought about by changes in the environment. The

real causes of abundance peaks are many known and unknown antecedent factors, some of which will be discussed below for the various species concerned. Consideration must also be given to the possibility that the abundance peaks are fortuitous, or in other words are brought about by inadequate sampling of the population. Nevertheless, the regularity of several of the curves, recurring seasonal modes and the similarity of the curves for the fishes of the order *Heterosomata* indicate that sampling was adequate.

Since most of the data are presented in the form of curves the terms used in describing the variations in numbers of the various fishes will be those of a simple statistical curve.

It is implied in speaking of seasonal variations in abundance that they are more or less cyclic or rhythmical in nature, recurring from year to year. Flattely (1920) has pointed out that there are two types of biological rhythm, (1) those correlated with the environment and (2) those inherent in the organism, the latter being probably correlated with the age cycle. Several workers have shown that animals in the tropics have definite breeding rhythms, although the seasonal differences are very slight or none. The work of Yonge (1930) on the Great Barrier Reef is an example.

Pearse (1926) summarizes the matter in these words: "The annual cycle of many species of animals is made up of a series of stages in a characteristic life history or of a characteristic series of periods of rest and activity which are closely correlated with seasonal succession. Long established correlations operate in such a way that seasonal environmental changes serve to stimulate animals to appropriate activities or inactivities and cyclical physiological changes within animals prepare them to react properly with recurring seasonal events."

Elton (1927) states that: "The numbers of very few animals remain constant for any great length of time, and our ideas of the workings of an animal community must therefore be adjusted to include this fact."

Before going further it is well to call attention to Verworn's (1913) pertinent criticism of the word *cause* as often used by workers in science and others. He points out that the happening of any event is preceded by an infinite concatenation of antecedent factors, the removing of any of which would preclude the happening of the event. He further points out that the seizing upon of any one of these conditioning factors and calling it a cause in contradistinction to the other factors which are of equal value in conditioning the given event is an improper and false usage. This is especially the case in ecological work where there are so many interrelationships seen and unseen. Nevertheless, the usage of the word *cause* is so common and ingrained in the language that it will be used with the above reservations in mind.

A complete answer to the many questions arising from the data would entail a complete study of the biotic associations of the whole area. The difficulty of attainment of this ideal have been pointed out by Elton (1927).

whose remarks relate to succession, but are applicable and are quoted here, ". . . it is almost impossible to make even a superficial study of succession in any large and complicated community, owing to the appalling amount of mere collecting which is required, and the trouble of getting the collected material identified. When one has to include seasonal changes throughout the year as well, the work becomes first of all disheartening, then terrific and finally impossible." Elton then counsels that the ecologist choose simple communities for they are just as valuable for purposes of theory. This, of course, is of little satisfaction to the marine ecologist or fisheries zoologist, who of necessity must work in a given area where particular species reside and which is never simple.

In the face of the impossibility of working out the problem as a whole, a given set of phenomena such as seasonal variations in abundance must be selected and as many legitimate conclusions drawn from them as possible. It seems very probable that only by such forward inching movements will the life histories of fishes and their interrelationships with their environment be worked out.

SCIAENIDAE

An understanding of the vastness of animal numbers and the numerical relationships of the various species or groups will probably often result in changed viewpoints. Elton (1927) has pointed out the interesting censuses of soil fauna at the Rothamsted Experimental Station, where it was found that the generally neglected springtails were more numerous than the flies and about seventy-eight times as numerous as the lepidoptera.

Censuses of fishes in a large area are very difficult and probably will always be relative. However, data have been presented (Gunter, 1938) which indicate that the *Sciaenidae* is one of the most successful families in this area from a numerical standpoint.

Micropogon undulatus (Linnaeus)

The croaker is the most abundant fish in trawl catches on the Louisiana coast. It is numerous at all times and at certain seasons its numbers are enormous. Millions are caught every year by shrimp trawlers.

Figure 2 shows that in 1932 there was a summer maximum abundance for this species on the inside extending from May to September with a mode in June. In 1933 it came earlier and did not last as long. The fish taken on the inside were small to medium-sized and grew rapidly as the summer progressed. On August 1, 1932, croakers taken on the inside ranged from 7.8 to 12.0 cm. in length. During the middle of October they ranged from 9.0 cm. to 13.5 cm. in length. On July 31, 1932, croakers caught on the outside ranged from 9.0 to 13.2 cm. in length while in the middle of October they varied from 8.5 to 17.5 cm. In the open gulf, as shown by the curve, there was a summer plurimum extending from May to October in 1932 with a peak

in September. The two curves rise and fall reciprocally in the summer of 1932 and from May to July in 1933.

It is evident that the fish pass to the outside as they grow larger. They do not return to the bay in winter and probably go out to deeper water. Pearson (1929) stated from general observations that there is a noticeable migration of croakers from the bays to the gulf in September. The curves here for 1932 show this and in 1933 the migration came earlier. The chief spawning month is in November according to Pearson and it seems that as the fish grow up they migrate to the gulf and congregate in preparation for spawning.

Post-larval and very small specimens occur in the bay in the winter and are abundant in February and March. Pearson has taken them from October to February in Texas, which indicates a long spawning season. The young and post-larval forms were never taken except in the bay and most abundantly in the headwaters. Pearson has shown that the croaker spawns on the outside near the passes and has observed the young making their way into the bay in large schools. The very young have been taken fifteen miles offshore in nets at Beaufort, North Carolina (Hildebrand and Cable, 1930) and it is probable that they spend some time in the plankton before starting inshore.

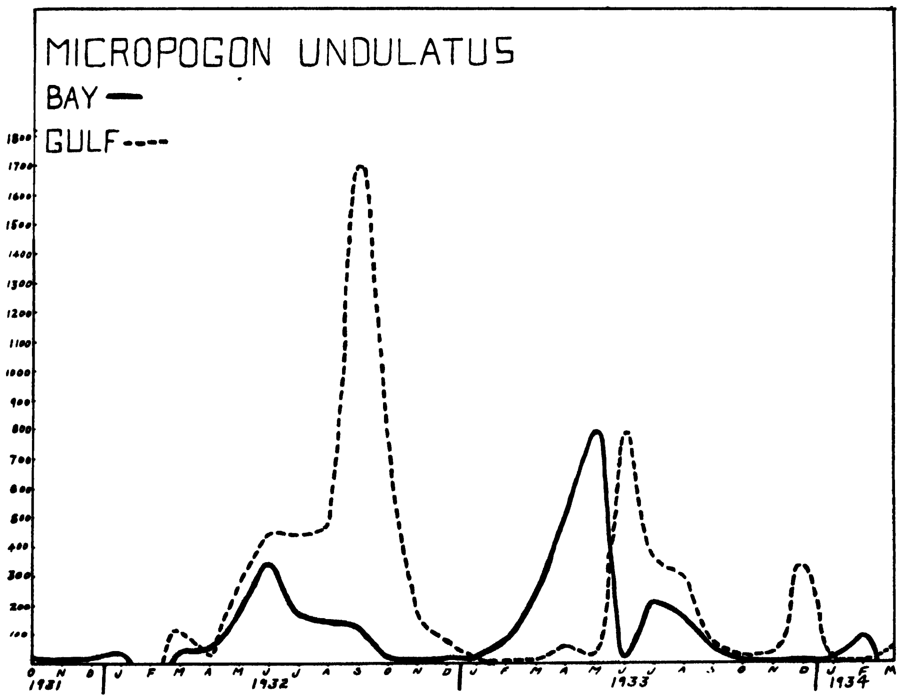

FIGURE 2. All plotted graphs are of abundance variations of the stated species of fishes, as determined by the catch in otter trawls from October, 1931 to March, 1934. The months and years are given along the x-axis. The figures along the y-axis are the average number of fish caught per haul each month. Separate curves for the bay (—) and gulf (---) waters are shown.

In the trawls only the largest animals were taken at this distance from the shore.

It is interesting to note that during the winter and early spring the water in the upper part of Barataria Bay becomes very fresh. The young seem to be more cold-resistant than the older fish for they are caught in the late winter in shallow water when the latter are offshore in deeper water. This phenomenon has been noted before for the croaker and the spot by Hildebrand and Cable.

Stellifer lanceolatus (Holbrook)

This fish ranks next to the croaker in numbers in trawl catches. It is very small and does not grow much larger than 12 cm. in length. It is of no commercial importance, but is probably of great ecological importance in the animal associations of this area.

Fish of this species seem to prefer the shore waters of the open gulf, for they were seldom taken in large numbers far from land and were usually scarce on the inside except in September, 1932, and July and October, 1933. This time also corresponds to the greatest abundance in the gulf for these years.

There was a peak of abundance on the outside in the summer of 1932 and 1933 as shown by Figure 3. Animals ripe enough for stripping were taken in April, May and June, 1933, and as the animals taken at this time are adult it is possible that this abundance is due to congregating of breeding individuals. Welsh and Breder (1923) say that May and June are the principal spawning months on the Atlantic coast. The post-larval and small animals come into the fishery to maintain the peak noted in late summer for both the inside and outside. These grow rapidly during the summer and fall. Welsh and Breder state that maturity is reached in one year, and also say that the largest fish they observed was two and one-half years old.

The writer's observations, which unfortunately are not checked by adequate total length measurements, were that many of the larger animals disappear after spawning and it seems that this fish has a short life cycle. Scale readings and total length measurements will determine the point. Pearson (1929) states that the related species, *Micropogon undulatus*, spawns for the first time in the second year and that few appear to live after that. Two fish taken on August 1, 1932, in the bay measured 8.0 and 10.3 cm. respectively. Seventy fish taken in the gulf in October ranged from 5.0 to 12.0 cm. in length and most of them were below 10.0 cm.

Menticirrhus americanus (Linnaeus)

The figure (4) for the black mullet shows a very slight peak in numbers on the inside in September and October in 1932, and October and November in 1933. It is clear that the numbers of this species fluctuate in the gulf, but the figure shows that they reach a maximum in the winter. There is a small

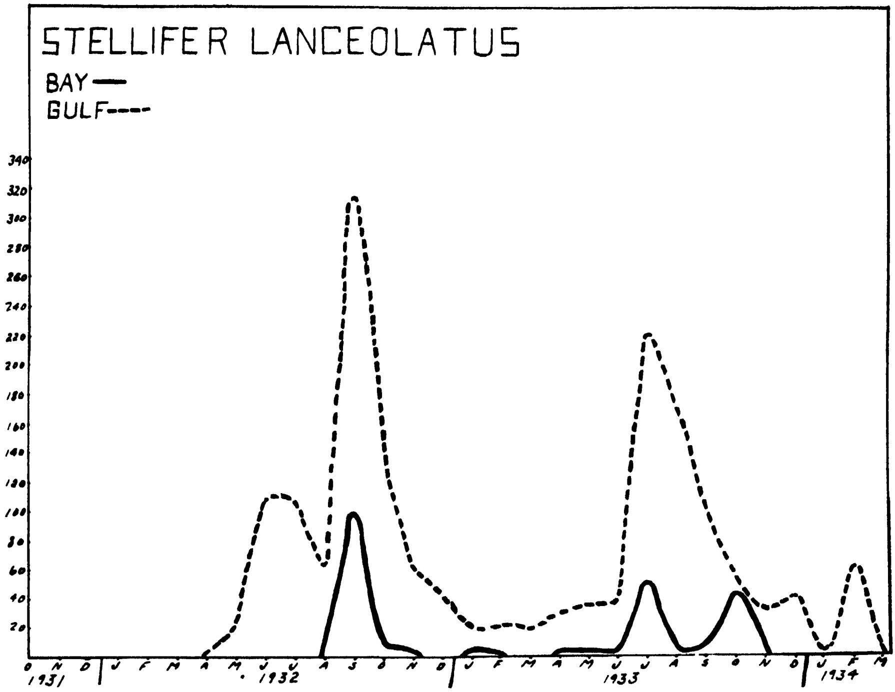

FIGURE 3. See Figure 2 for explanation.

peak in September and October of 1932 corresponding with that on the inside. The time of greatest abundance was in February and March, 1933, on the outside. Fish with well-developed roe were taken in April, May and June, 1933, in the gulf. Smith (1907) states that *Menticirrhus americanus* spawns in June at Beaufort, North Carolina. Hildebrand and Cable (1934) state that the season at Beaufort is from April to August or September and that fish with well-developed roe are most common in May and June. Smith also states that the species is most abundant in the spring and is present in schools in the fall. This corresponds with the findings in Louisiana which show the black mullet is most common from September to March. The curves also show clearly that the fish prefers gulf waters.

Bairdiella chrysura (Lacépède)

The yellowtail, as shown in Figure 5, fluctuated in numbers in the gulf and was not common. In January, 1932, there was a marked peak of abundance in Barataria Bay. The following year this was not the case, but in January, 1934, the mode was repeated on a smaller scale. The explanation for this is not known. There is a slight peak on the inside in August, 1932, and a large one during July of the next year. These modes may have been due to the migration of fish after spawning.

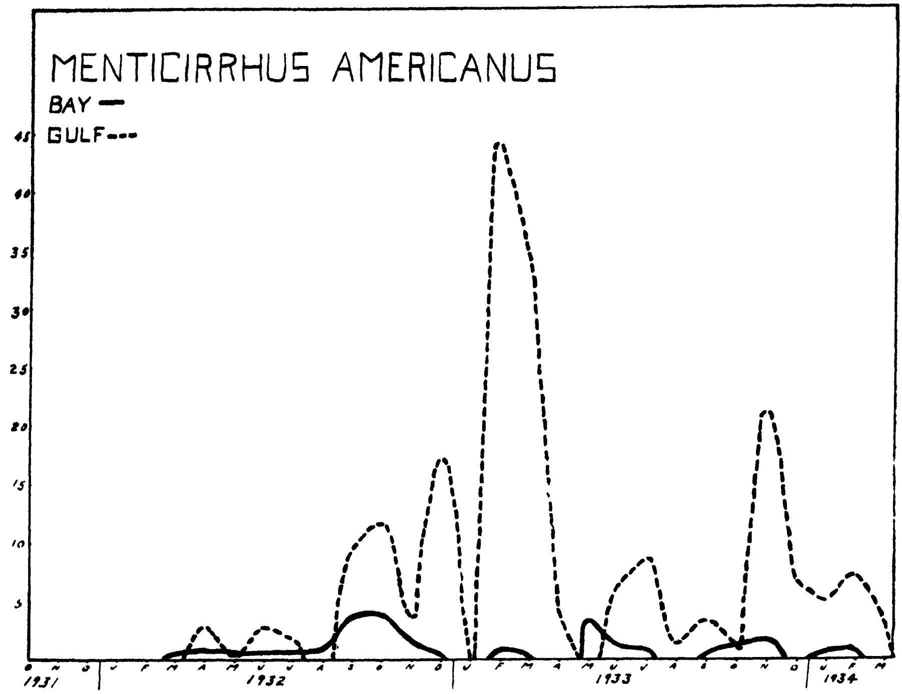

FIGURE 4. See Figure 2 for explanation.

Females ripe enough for stripping were taken in April, May and June, 1933, both in the bay and in the gulf, which agrees with the statements of Hildebrand and Cable (1930) that the spawning season is from the end of April to the end of June at Beaufort. The peak on the inside was made by small individuals which probably developed from this spawning. Unfortunately very few measurements were made. Four fish taken in the bay on August 1, 1932, measured between 8.3 and 9.0 cm. in length. Thirty-eight fish taken from 2 to 3 miles out in the gulf on July 31 of the same year measured from 10.2 to 13.3 cm. in length. Twelve fish taken in the bay from October 14 to 16, 1932, ranged from 9.0 to 12.0 cm. in length.

Hildebrand and Cable (1930) found that *Bairdiella chrysura* grows amply large enough to sexually mature at the age of one year, although it is not actually known that it spawns at this age. Probably the life history is short and somewhat like that suggested for *Stellifer lanceolatus*.

Leiostomus xanthurus (Lacépède)

Figure 6 shows that there was a decided abundance mode of this species in the gulf during June and July, 1932, with a slighter peak at the same time on the inside. The increase in numbers first began in the gulf in April, 1933, instead of May as in 1932. It roughly corresponds to the mode of the latter

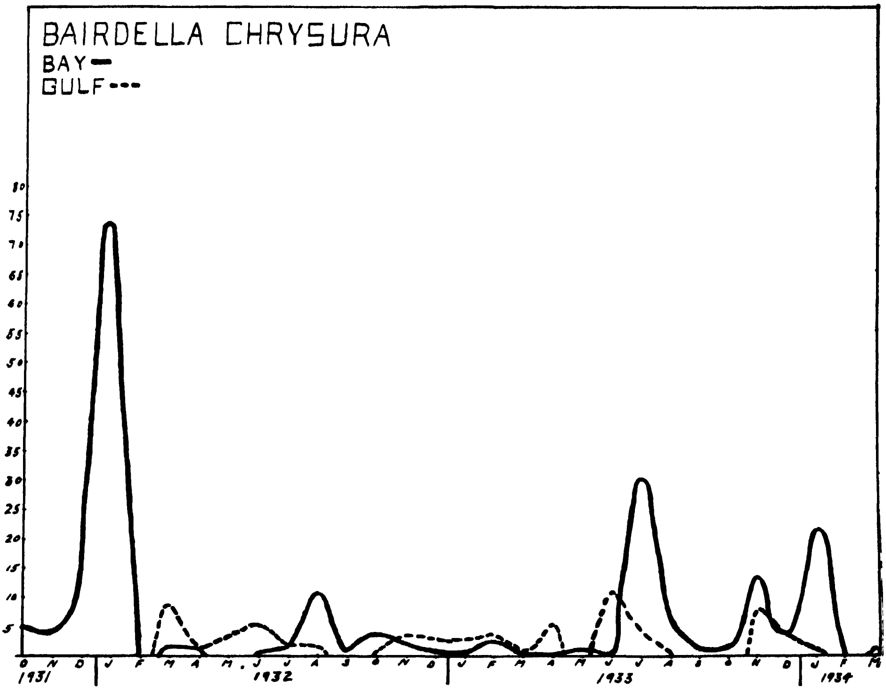

FIGURE 5. See Figure 2 for explanation.

year except that it is a little longer and the abundance is most pronounced on the inside and in August rather than in June as in 1932. The fish is probably adapted to both environments but is sensitive to changes or has "preferences," so that the greatest numbers may be in the gulf in one summer and in the bay during another, depending on unknown factors.

The individuals making up the summer abundance peak first appeared in the gulf. They were from 2.5 to 3.5 cm. in length and had evidently been spawned a few months before. Pearson (1929) states that in Texas the spot spawns from late December to the last of March with the height of the season in January and February. Possibly the peak noted in January, 1934, was made by spawning fish. It was not seen in other years.

The young fish grew rapidly and appeared to attain adult size by the end of the summer, when their numbers began to decline. Pearson (1929) noted this rapid growth in Texas. In Louisiana forty specimens taken in the bay in August, 1932, measured from 9.5 to 13.5 cm. in length. Sixty fish taken from the bay in October, 1932, measured from 11.0 to 16.0 cm. in length.

The curve shows that just before each summer increase in numbers the spot entirely disappears. This agrees with the statement of Pearson that after the first spawning most of the fish apparently perish. The disappearance noted may be explained on the hypothesis that adults died after spawning and

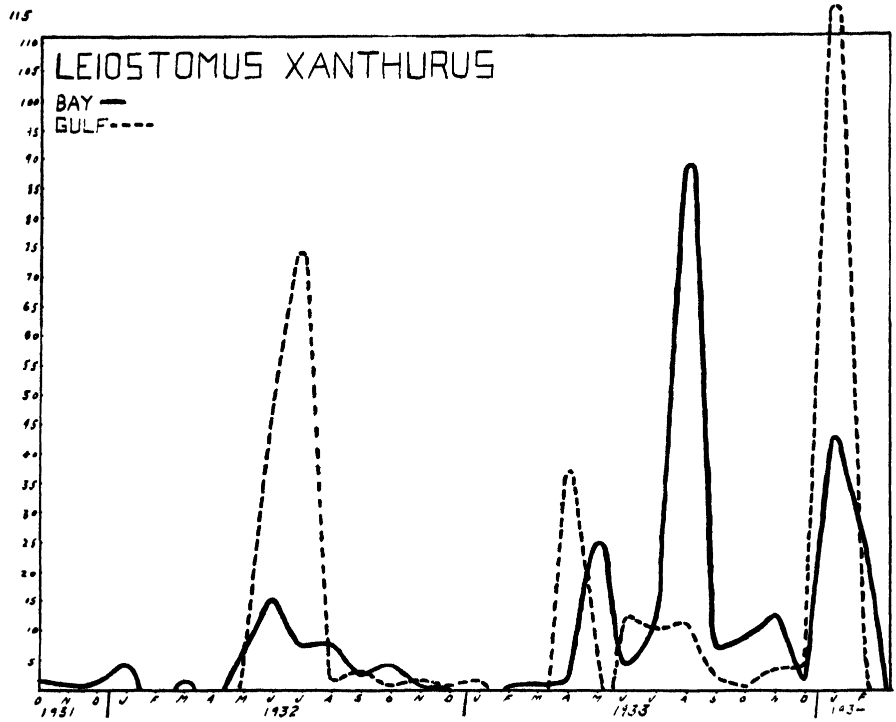

FIGURE 6. See Figure 2 for explanation.

the young are not immediately taken in the trawls because of their small size. Apparently the life cycle of *Leiostomus xanthurus* is short.

Larimus fasciatus (Holbrook)

Table 1 shows that the banded croaker was rarely caught in inside waters. Hildebrand and Cable (1934) state that they have no record of it entering the harbor or sound at Beaufort, N. C. In the gulf there was a slight increase in numbers in August, 1932. The same small increase was present in August, 1933. Hildebrand and Cable say that spawning takes place over the whole summer and begins as early as May at Beaufort. Post-larval animals were taken in seine hauls on the beaches in Louisiana during May, 1933, and it is possible that spawning begins here a little earlier, probably in April.

This fish is one of the smallest sciaenids, and unlike most members of the family in American waters is of no commercial importance. The total numbers at the time of greatest abundance were not large, but as the fish is relatively scarce at all times they are as marked as the greater increases are for more common species. The summer abundance is probably due to the fact that the young of the year attain size enough to be taken in the trawls at that time. Five individuals taken in the gulf in October measured from

12.0 to 14.0 cm. in length. According to Hildebrand and Cable some of the young of the O class attain a length of 7.0 cm. by July at Beaufort.

Welsh and Breder (1923) indicate that this species is one of the most abundant on the shores of the Gulf of Mexico. The statement probably applies to Florida, for it is not true of Louisiana.

OTOLITHIDAE

Cynoscion arenarius Ginsburg

The curve for the white trout on the inside, pictured in Figure 7, shows a wide mode from June to October which fluctuates strongly from month to month in 1932. As cooler weather approaches most of the fish depart for the open gulf. This fluctuation may be due to a back and forth movement from one part of the bay to the other or more likely from the inside to the gulf. This movement may be due to a sensitivity to some environmental condition. An analysis of hydrographic data collected at the time of this study may shed more light on the subject. In the winter of 1932 the fish were numerous in the gulf although not so much as in June and July. In the winter of 1933 there was a marked mode with a peak in December which exceeded the summer peak on the outside for that year with the high point in August. There is also a marked fluctuation on the outside in winter.

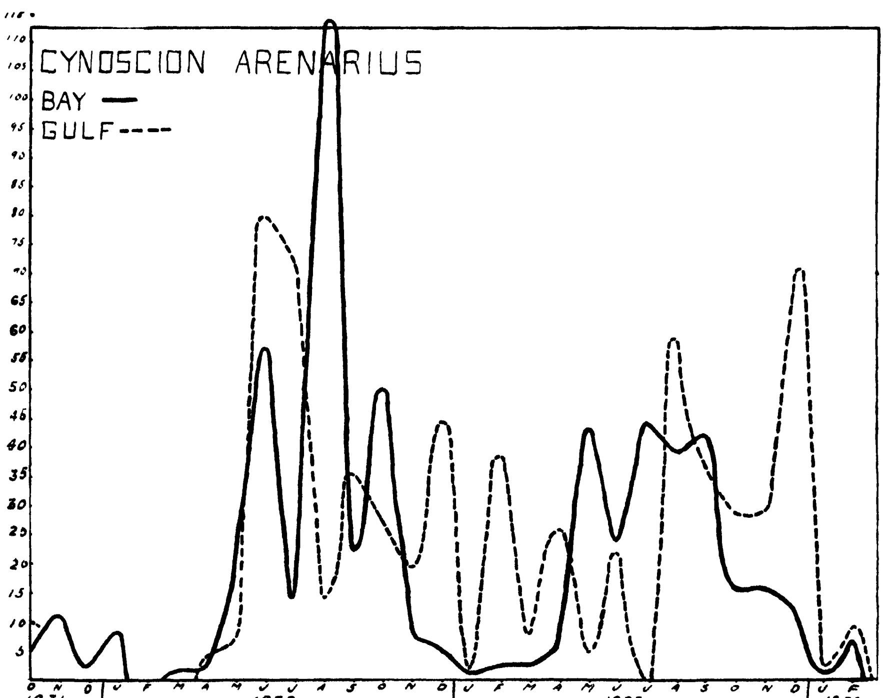

FIGURE 7. See Figure 2 for explanation.

Higgins and Pearson (1927) state that the height of the spawning season for *Cynoscion regalis* is reached in June in North Carolina and that season is over by August 10. *C. arenarius* with well-developed roe were taken in Louisiana in April, May and June of 1933. It seems that the spawning season for the two species corresponds roughly and it is possible that the high peak of abundance in June and July of 1932 in the gulf was due to breeding animals.

Small fish were taken in large numbers during the fall in inside waters. As the fish grew up they passed into the gulf. This is shown by the fact that the inside curve for winter months drops almost to the base line. In August, 1932, eighty-seven fish from the bay measured from 7.5 to 14.0 cm. in length. In October 117 fish taken in the same place ranged from 5.0 to 15.0 cm. in length, while forty from the outside measured from 10.5 cm. to 20.0 cm. in length.

Cynoscion nothus (Holbrook)

Cynoscion nothus is a smaller species than *C. arenarius* and frequented the gulf almost solely. Its abundance increased directly as the distance offshore up to six or eight miles. The reverse is true of the latter fish for it was more common in the bay. Eighteen hauls made in the summer of 1933 one mile offshore gave 62 *C. nothus* while 18 hauls made on the same days, three to six miles offshore gave 223 fish. Ginsburg (1931) has previously called attention to this distributional difference of the two species. *C. nothus* was taken in the bay during the months of December, 1932, and January and May, 1933. In all probability it is sensitive to temperature rather than salinity, like the mackerel in the Black Sea as observed by Galtsoff (1924). It is to be noted that the salinity of the bay at this time of the year is much lower than that of the fish's usual habitat. Table 2 shows a summer peak of abundance on the outside in August, 1932, and July and August in 1933, somewhat like *C. arenarius*. It was not as common as the latter fish.

Cynoscion nebulosus (Cuvier and Valenciennes)

Unlike the preceding species the largest specimens of *C. nebulosus* were not taken in the trawls. Smaller fish from 2.5 to 20.0 cm. were often taken on the inside. Higgins and Lord (1926) quote fishermen as saying that spotted trout are most common in December, January, February and March in Texas, which agrees with the findings in Louisiana. They also quote notes of Simmonds, saying that the fish spawn from May to early September. Pearson (1929) states that the spawning season extends from March to October and the height of the season is reached in April and May in Texas. He also shows that spawning takes place in inside waters. Two large females with hard roe were taken by the writer at the mouth of Barataria Pass in the latter part of May, 1933.

In Louisiana (Figure 8) a few stragglers were taken in the gulf in March, 1932, and again in January and February, 1933. Smaller individuals, if not adults as well, prefer inside waters. A marked increase in numbers was found in the winter with January as the peak month in 1932 and 1933. February was the month of greatest abundance in 1934. These modes were caused mostly by small fish which obviously were spawned the previous spring and summer, although other sizes were not uncommon. There was much overlapping of various sizes which Pearson (1929) says is due to a protracted spawning season, making it difficult to sharply identify year classes. Like the croaker the young of this fish were found to be very tolerant of freshwater and low temperatures. Numbers increased from the mouth to the headwaters of the bay, where they attained a maximum and at times predominated in the catches, even exceeding the ubiquitous croaker. Likewise, larger specimens were taken nearer the gulf, but never in as great numbers.

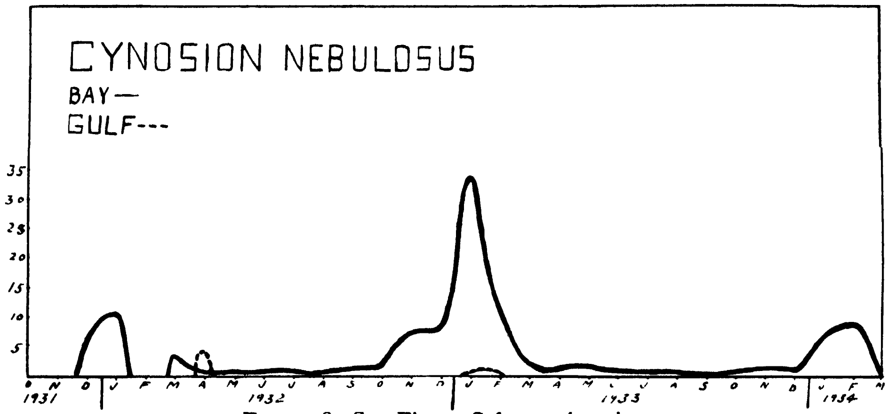

FIGURE 8. See Figure 2 for explanation.

POLYNEMIDAE

Polynemus octonemus (Girard)

In 1932 the threadfin appeared in May both in the bay and the gulf as shown by Figure 9. In April, 1933, it was first taken in plankton tows in the gulf. The fish were then about 5 cm. in length. They grew rapidly and were about twice that size by the end of the summer. This species is only a summer and fall resident and its arrivals and departures were as regular as those of migratory birds. The figure shows that it left the area studied in October in the years 1932 and 1933. The period of residence is from April or May to October. The 1933 abundance in the bay was due to large schools of small fish which were often observed and caught in dip nets at night, near the electric lights of a shrimp platform.

Piecing together the story from the facts at hand, it seems that the young which were spawned the previous fall or winter first appeared offshore in the

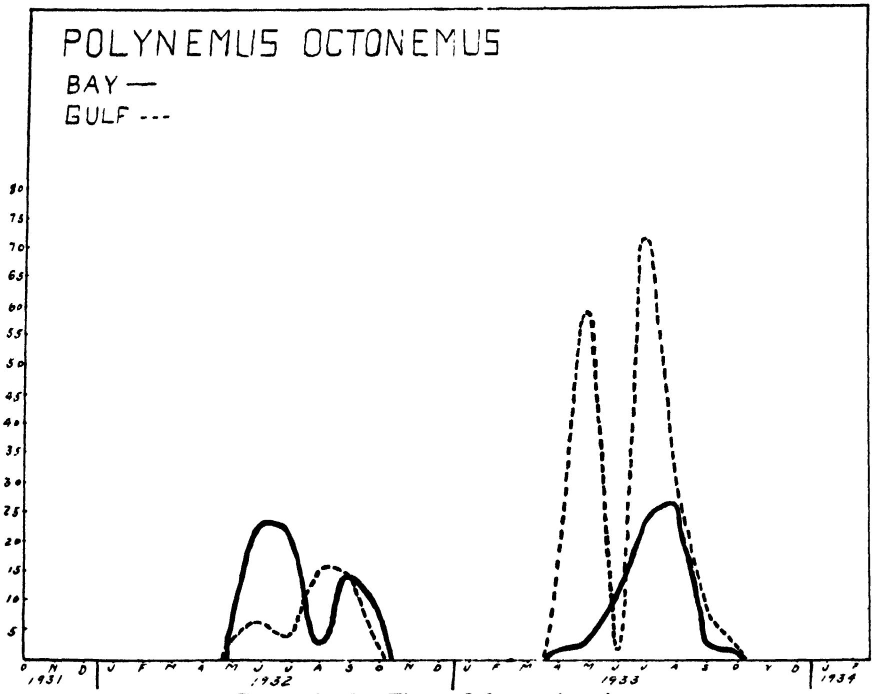

FIGURE 9. See Figure 2 for explanation.

spring and came into the bay forming the summer abundance peak noted for two consecutive years. Here they grew rapidly and returned to deeper water in the fall. Ninety-one fish taken in Barataria Bay in August, 1933, ranged from 7.8 to 13.5 cm. in length. Four fish taken there in October measured from 11.5 to 13.0 cm. in length, while fourteen fish taken in the gulf at the same time ranged from 13.0 to 15.0 cm. in length. Whether this species spawns close to shore or in deep water is unknown, but the latter supposition is the more probable. At any rate, the young were not caught until the following spring.

TRICHIURIDAE

Trichiurus lepturus (Linnaeus)

Figure 10 shows a summer peak of abundance for the cutlass fish in the gulf, beginning in April in 1932 and in July, 1933, with both extending through September. There is also a smaller peak in the winter extending from November to March or April for both 1932 and 1933. The curve fluctuates but is similar for the two years. In 1932 the fish was not plentiful in the bay, but compared to its winter population of that and the year before it was at a peak paralleling that on the outside for the same time. In 1933 this peak was well apparent and extended from May to October.

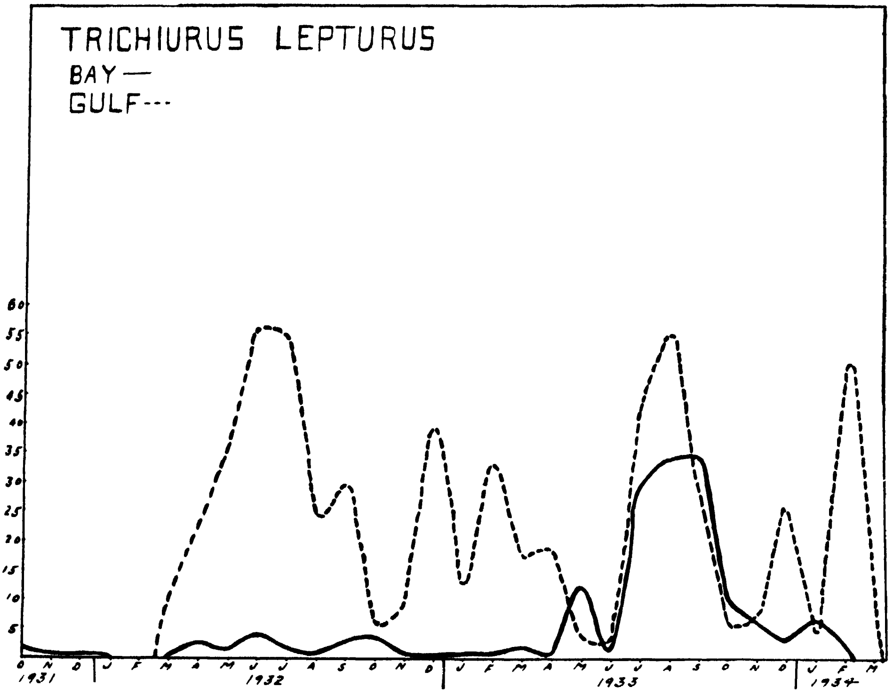

FIGURE 10. See Figure 2 for explanation.

Smith (1907) states that spawning takes place in the summer, for a ripe fish was taken at Beaufort in August. In the last week of April, 1933, the very attenuated young first appeared in the catches in the gulf. Perhaps they were spawned in the previous summer or fall. No measurements were made but general observation indicated that they composed most of the catch on the inside for that year. The peak began in May immediately after the first appearance of the young. In the bay they preponderated, but size limits were very wide in both localities and it is probable that several year classes were present. It is evident from the figure and observations here related that the young are probably spawned on the outside, pass to the bay nursery grounds during the summer and return to the gulf in the fall. The winter modes were at peaks in December and February for two consecutive winters. This fish is more common in the gulf than in the bay, contrary to the figures given by Gunter (1938) where those for the outside are erroneous.

STROMATEIDAE

Poronotus triacanthus (Peck)

The butterfish was never taken in large numbers. It seemed to prefer gulf waters and when caught in the bay was more plentiful near the lower end. In the late winter and spring of 1933 it was much more plentiful than in the

preceding year (Table 2). This group was composed chiefly of half-grown fish. The period of abundance in the gulf extended from February to June. The previous year and the following year this numerical increase was not noted, so it cannot be said whether or not it is typical of the life cycle.

CARANGIDAE

Caranx hippos (Linnaeus)

Table 2 shows that the jackfish was caught in small numbers in the bay from July to September in 1932 and July to November in 1933. On the outside it was most common in the summer months with an occasional straggler in spring and fall. All specimens taken were of small size, the largest not exceeding 15 cm. in length. Very often the small fish were taken from the bell of the jellyfish, *Stomolophus* sp. Adult fish were common in the summer three or four miles offshore. In the winter they were absent and evidently passed out to deeper water.

Selene vomer (Linnaeus)

Table 1 shows that the lookdown was not caught in the bay at all. It was absent from the gulf in winter at the points visited. Its appearances were sporadic, though in October, 1931, and September, 1932, it became plentiful. There may be an abundance peak at this time which cannot be detected due to the fish's sporadic appearances. Hildebrand and Schroeder (1928) observed this species in Chesapeake Bay only in September and October.

Vomer setapinnis (Mitchill)

Figure 11 shows that in October, 1931, and in September, 1932, and October, 1933, the moonfish was numerous inside. Hildebrand and Schroeder (1928) observed that this species was most common in Chesapeake Bay in September and October. The figure also shows that the fish was absent from the bay in the winter and spring. This is the season of low temperature and salinity. Fish taken in the bay were of all sizes and the numbers cannot be attributed to a migration or sudden appearance of the young. This species frequents the open gulf, and it seems that the increased catch at this time is a result of a general ingress to the bay at a season when the water conditions are suitable and comparable to those of the inshore gulf. The fish was always more common at the lower end of the bay. The curve for the gulf shows a rise in numbers in March, 1933. Beginning in July there is a mode with a peak during October. There is a peak on the inside at the same time. Then the fish depart for deeper water. It is clear that this species is most numerous in the fall. Yarrow (1874) recorded the fact at Beaufort, North Carolina, many years ago.

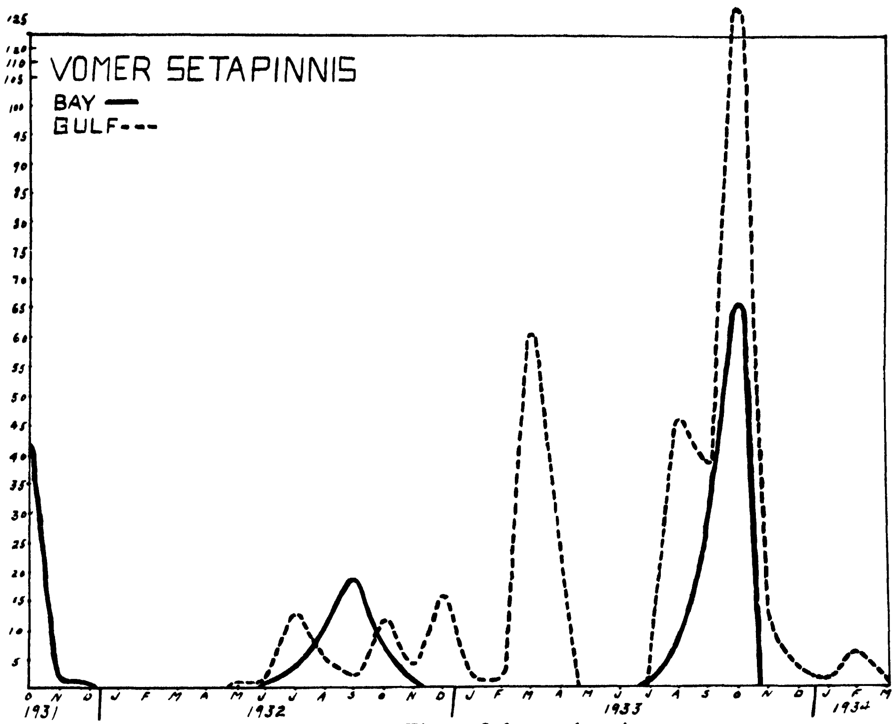

FIGURE 11. See Figure 2 for explanation.

Chloroscombrus chrysurus (Linnaeus)

The bumper was taken in the bay in October, 1931, and August, September and October in 1932. Like *Vomer setapinnis* it was caught near the lower end of the bay at a season when the hydrographic conditions were comparable to those of the shallow water of the gulf. At all other times it was absent. Table 2 shows that the animal was taken chiefly in the fall in the gulf. There seems to be a peak of abundance at this time. It was quite common in March, 1933, although it was not found the preceding or following month. This may have been due to migration along the coast.

CLUPEIDAE

Brevoortia patronus (Goode)

The menhaden is quite common and is possibly more numerous than trawl catches indicate for it is a plankton feeder and not as susceptible to capture as bottom feeding fishes. The writer has observed large schools feeding near the surface in Caminada Bay where they wheeled, turned and swerved from side to side in perfect unison, all the while with mouths agape and lower jaws thrust forward.

Figure 12 shows that this fish was caught much more in the bay than outside. Individuals from inside were mostly immature and it is possible that

adults were present in larger numbers in the gulf. During the months of June and July in 1932 and June, 1933, the menhaden was scarce inside and was taken more commonly in the gulf. In 1932 there was a peak in the bay in January. The following year the peak came in December and January and in 1934 it came in January and February. This is ample data to establish the fact that there is an abundance peak for this fish in the bay during the winter, which is characteristic of the life history of the species. The winter mode was made up of small fish which must have been spawned the previous summer and fall. Smith (1907) records that large schools of young *Brevoortia tyrannus* are present from December to March near Beaufort. Hildebrand and Schroeder (1928) say that *Brevoortia tyrannus* seems to hatch in the fall in Chesapeake Bay. The increased numbers caught in midwinter, indicated in Figure 12, are possibly a result of migration of such individuals from nursery grounds near the shore to the open bay. They grow rapidly and probably by midsummer most of them pass to the outside, as the curves indicate. Fish taken on the outside were usually adult or nearly adult in size. Smaller individuals were sometimes caught near the shore.

Signalosa atchafalayae (Evermann and Kendall)

As shown by Tables 1 and 2 this fish was occasionally taken in the gulf, although most of the time it was completely absent. Like the menhaden it was

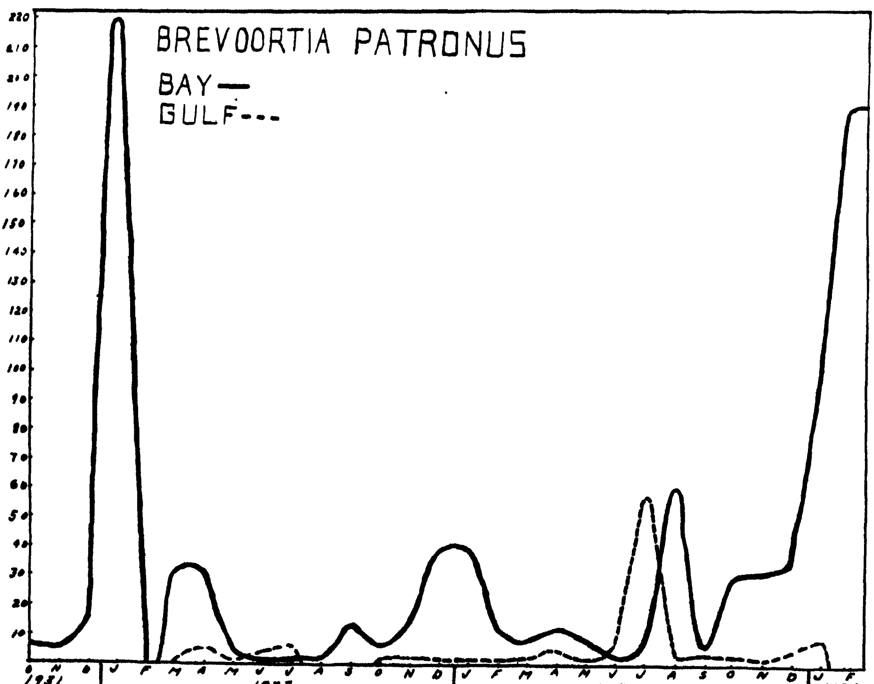

FIGURE 12. See Figure 2 for explanation.

taken most often in bay waters. In 1932 it was abundant in December. In the previous year it was more numerous in January; in 1934, in January and February. There was also a slight increase in numbers in the fall of 1933, as in 1932. The fish taken in midwinter were mostly small and were probably spawned the summer before. The seasonal variation in numbers for this species is much like that of its relative, *Brevoortia patronus,* previously described.

ENGRAULIDAE

Anchoviella epsetus (Bonnaterre)

Anchovies were very common, but relatively few were caught in the trawl because of their small size. On numerous occasions the writer has seen them thrown into the water in hundreds by a slight shake of the net. They probably have a prolonged spawning season during the summer and fall, for the young appear by millions in the late winter and spring. Hildebrand and Cable (1930) state that the spawning season at Beaufort, N. C., is from May to August. Specimens with well-developed ovaries were taken in the gulf in May.

In 1932 (Figure 13) the fish were very numerous on the inside from December to May with the peak in April. Almost all were small. On the outside the mode extended from March to June with the peak in May. The

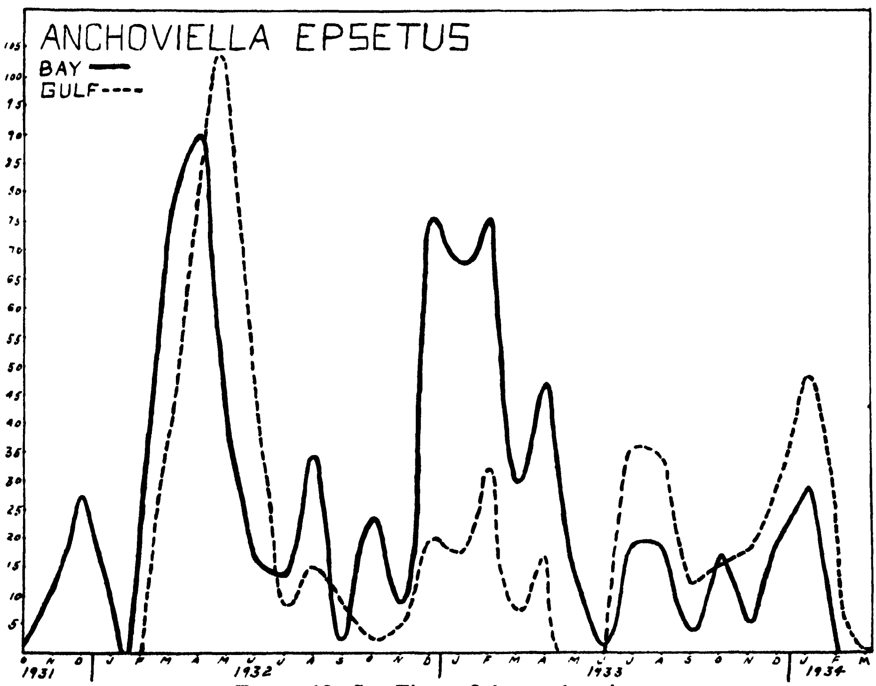

FIGURE 13. See Figure 2 for explanation.

two following years there was a peak in both the bay and gulf in midwinter which declined in March in 1933 and February, 1934. Small post-larval fish make up the winter abundance. Larger fish make up the summer population. Post-larval anchovies were taken in large numbers in the bay, while in the gulf they were taken more rarely. The fish caught in the open sea were of larger size than those of bay waters. They probably spawn in the gulf in shallow water. It was seldom that adults were taken on the inside. During the summer of 1932, 216 fish from the bay measured from 3.5 to 10.5 cm. in length while 26 from the gulf ranged from 4.4 to 11.5 cm. in length.

ARIIDAE

Bagre marinus (Mitchill)

Figure 14 shows that the gaff-topsail catfish was abundant in September, 1932 and 1933, both inside and outside. The curve for the hardhead catfish, *Galeichthys felis,* shows the same picture except that in 1933 the peak was in October for the inside with a high point in July for the outside. In both species this inside peak was made to a large extent by small fish, which were carried about as eggs and hatched in their father's mouths during the summer.

Males of both species carrying eggs were first taken in Barataria Bay the 12th day of June in the 1933 season. At the same time large schools of

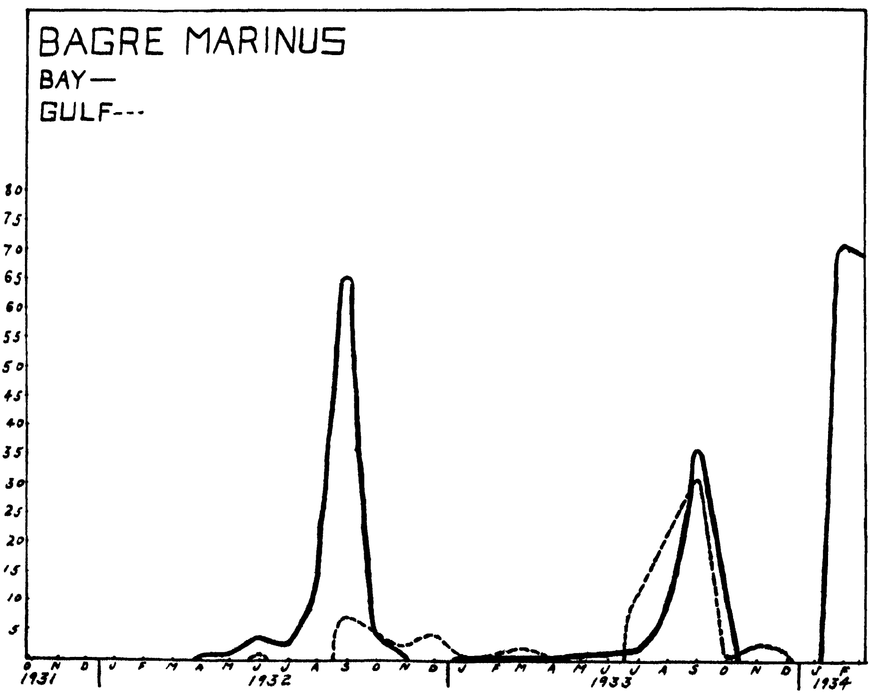

FIGURE 14. See Figure 2 for explanation.

"hardheads" were reported to be "breeding" in Caminada Bay. The writer did not observe these schools but saw fish caught there at that time, which had eggs in their mouths. No fish which were carrying eggs were caught in the gulf. This is similar to the case of *Galeichthys felis* (Lee, 1937). The figure shows that after September most of the fish went to the gulf. They returned again to the bay the next May and June prior to spawning. February, 1934, is an exception.

Galeichthys felis (Linnaeus)

The hardhead is more common than its close relative, the gaff-topsail. The abundance peaks for September, 1932, and October, 1933, have been discussed with those for the former catfish. These fish very often go in schools and evidently move about quite a bit. A number of *Galeichthys felis* spend the winter in the bay (Figure 15). This is contrary to the case of *Bagre marinus*.

GADIDAE

Urophycis floridanus (Bean and Dresel)

Tables 1 and 2 show that this species was present in March and April, 1932. It was present from January to March in the gulf in 1933, and from

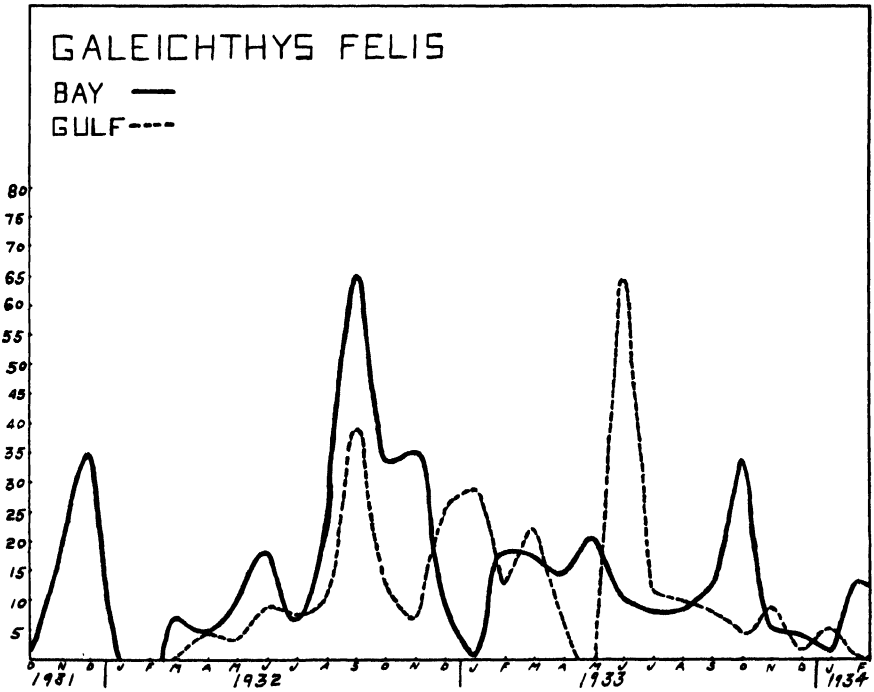

FIGURE 15. See Figure 2 for explanation.

December, 1932, to May, 1933, in the bay. It was caught on the outside in February and March, 1934. It is clear that this fish appears inshore only during the cooler months of the year. It is interesting to note that the winter of 1931-32 was exceptionally mild, except for one cold spell in the month of March during which freezing temperatures extended to the coast. *Urophycis floridanus* appeared after the cold spell. Jordan and Evermann (1898) noted the winter appearance of this species around Pensacola. Hildebrand and Schroeder (1928) noted the same thing for *U. chuss* in Chesapeake Bay. *U. floridanus* is a deep water species. It was present in Barataria Bay in winter and early spring when the salinities were very low. Although it is a salt water denizen it seems to be tolerant of low salinity and is probably kept out of the bay in summer by the higher temperatures in shallow waters.

HETEROSOMATA

Of the seven species of this order caught, namely, *Trinectes maculatus, Achirus lineatus, Citharichthys spilopterus, Etropus crossotus, Symphurus plagiusa, Paralichthys lethostigmus,* and *Ancylopsetta quadrocellatus,* the curves for all except the last two and *Achirus lineatus* have a very outstanding peak in September, 1932. The last two fishes were caught too rarely for any conclusion to be drawn about them, and *Achirus lineatus* had the peak in October rather than September. The next year the mode fell in October and was so slight for some as to be scarcely noticed. In 1934 there was also a mode for March on the outside, common to the same species except for *A. lineatus.* It is probable that this last mode was caused by spawning animals.

Whatever the affinity or relationship which causes the close resemblance in this phase of the life history of these flatfish it must be quite strong for it embraces five species in three different families. The number of species and the similarity of the curves for three years and at different times of the year make it impossible for the phenomenon to be a matter of chance. The curves for each species being so similar, they were combined and presented in Figure 16.

Citharichthys spilopterus (Günther)

This species was caught very little in the gulf. In the bay it was not plentiful and in some months was not caught. In September, 1932, and October, 1933, the abundance peak was marked as was the case with close relatives of the fish. This was not caused by young individuals. Possibly it was caused by the migration of adult and half-grown fish from shallow to deeper water before the approach of winter.

Etropus crossotus (Jordan and Gilbert)

The abundance variation of this species is practically the same as that for *Citharichthys spilopterus,* with the difference that there was a peak on the

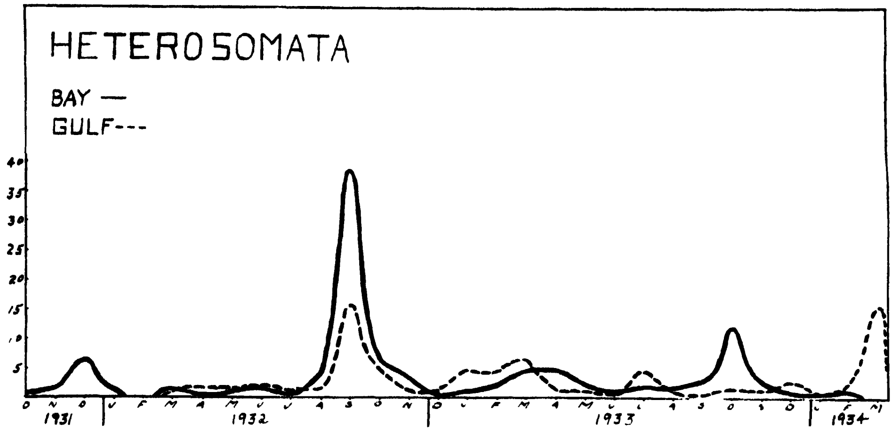

FIGURE 16. See Figure 2 for explanation.

outside corresponding to that on the inside in September, 1932. It was numerous on the outside in July, 1933; just why is not known, and no such increase was noted in any other year.

Paralichthys lethostigmus (Jordan and Gilbert)

Rarely this fish was taken in the gulf. In the bay it was never plentiful in trawl catches. In April, 1933, numerous small fish from 5 to 10 cm. in length were taken on outside beaches in seines. From a month to two months later this species appeared in trawl catches at a size of 12 to 15 cm. in length. Hildebrand and Cable (1930) give evidence to show that *Paralichthys dentatus* spawns from September to April at Beaufort, N. C. Using the size of the young as a criterion it seems that the spawning of *Paralichthys lethostigmus* in Louisiana corresponds somewhat to that time, and the young grow amply large enough to be taken in the trawls the following year.

Achirus lineatus (Linnaeus)

This sole was not common either in the gulf or the bay. It was most numerous from September to November in 1932 with the highest point in October on the inside. There was no pronounced increase in the gulf. The following year the fish were most common in October.

Trinectes maculatus (Bloch and Schneider)

Like other members of the order *Heterosomata* there was a great abundance of the hogchoker in September, 1932, both in Barataria Bay and the Gulf of Mexico. In 1933 the peak was in October and for the inside only. There was a movement of fish from the gulf back into the bay in the spring in 1933. At this time a number of small fish were caught, which had evidently hatched the previous year, along with fish with well-developed ovaries, which were present in April, May and June, 1933. The spring catch was made up

of these two size groups. Hildebrand and Schroeder (1928) noted ripe fish in June, July and August in Chesapeake Bay.

Symphurus plagiusa (Linnaeus)

The appearance of the tonguefish was more or less sporadic both inside and outside. In both localities there was a marked abundance in September, 1932. In 1933 there was a slight increase in October for the bay only. In March, 1934, there was a peak in the gulf as there was for other species of the order. This fish is necessarily a slow swimmer and is therefore scarcely given to extensive migration from place to place. The sudden changes in abundance (Tables 1 and 2) must then be due to migrations to and from shallow water close to shore and the open bay or gulf. Small planktonic, symmetrical animals were taken in April, 1933, in the gulf. According to Hildebrand and Cable (1930) small fry of *Symphurus plagiusa* were present at Beaufort from May to October.

DASYATIDAE

Dasyatis sabina (Le Sueur)

The stingaree was seldom caught in the gulf (Table 2). In the bay it was caught more or less throughout the year. On February 4, 1933, seven males with milt were taken in one haul at the head of the bay. On February 16 another male in like condition was caught. On June 5, 1932, the writer observed a large female in moribund condition give birth to three young, one of which swam away after being placed in the water. These observations indicate that the approximate length of time the developing egg is held in the female is three or four months. Some writers say that this ray breeds all the year around, but no indication of this was seen.

DISCUSSION

The data presented are chiefly descriptive and are more valuable in this aspect than for purposes of analyses. Many unanswered questions have arisen, but the knowledge of these is an advance and some may be used as the starting point for future work.

For many species studied, namely, *Trinectes maculatus, Achirus lineatus, Citharichthys spilopterus, Etropus crossotus, Symphurus plagiusa, Cynoscion nebulosus, Brevoortia patronus, Galeichthys felis, Bagre marinus, Leiostomus xanthurus* and *Bairdiella chrysura,* there was a recurrent, sequential phase in the life history or annual cycle of the fish, when there was a sharp abundance mode. These fell at certain times of the year and can be expected to recur at about the same time in future years. Fishes of this group are differentiated arbitrarily from those such as *Micropogon undulatus* which has a wider period of increased numbers. *Polynemus octonemus* and *Vomer setapinnis*

came and went at certain times of the year, so that their arrivals and departures might be predicted with some accuracy.

The place or worth of observations on seasonal variations in abundance may be brought out by the words of Stuart Mill (1848), who said: "Of all truths relating to phenomena, the most valuable to us are those which relate to their order of succession. On a knowledge of these is founded every reasonable anticipation of future facts, and whatever power we possess of influencing these facts to our advantage." An example will illustrate. A study of the year groups of a fish might well be made at the time of its greatest numbers. If the abundance is due to the young, as was found here in many instances, studies of the numerical ratio of the zero year group to other groups, at the time of the peak, might be of aid in predicting the future abundance of year classes.

The time of greatest numbers in the annual cycle of a fish is that immediately following the hatching of the eggs. Thereafter there is a sharp decline due to the heavy mortality of the young, and the decline continues until the next reproductive period, although due to rapid individual growth the actual species mass may increase during part of this period. Yet the so-called peaks or abundance modes may be noted at a later date and may appear at different times for the different devices used for capture of the fish. In other words the peaks are to a certain extent dependent on the type of gear used, whether it be otter trawl, beam trawl, seine, plankton net or something else. Plankton nets will capture larval fish, but will fail to take larger specimens which may cause a peak of numbers in trawl hauls at a later date. A simple corollary of this fact is that the same collecting gear should be used from year to year in studying seasonal variations in the numbers of fishes.

In the study of variations in animal numbers from year to year or comparative abundance of species to species (Elton, 1927) it is of prime importance to recognize that there is an annual cycle of change in numbers taking place during the year and to know when it is taking place. An enumeration of animals at one time of the year would have to be compared to counts of other years at the same seasons. Several counts at different seasons of the year, compared to like counts in other years, would be much more valuable.

It is quite evident that the bay waters act as nursery grounds for many of the species studied here. The smaller fishes were practically always found inside, while larger individuals were taken in the gulf. Pearson (1929) has presented data to show that most of the *Sciaenidae* spawn in the gulf, and observations indicate that most fish discussed here did the same. Some of the evidence is indirect such as that for *Polynemus octonemus* and *Leiostomus xanthurus*, the small individuals of these species being taken in plankton tows in the gulf before being caught in the bay. Exceptions to this rule are *Galeichthys felis*, *Bagre marinus* and *Dasyatis sabina*, for which data have been presented, and probably *Cynoscion nebulosus*.

Certain fishes were found to frequent the bay waters, while others preferred the open gulf. This has been discussed under each species. More data on this point were given by Gunter (1938). It was noted that young individuals of many species preferred or possibly were able to stand low temperatures and salinities of the bay during winter better than older fishes.

It has been shown (Gunter, 1936) that from late spring to early fall is the time of greatest catches of fish in trawls and that the catches in the gulf become larger in the late summer. This apparently is due to the migration of young fish from the bay to the gulf as they grow up.

A very clear seasonal cycle and seasonal biological succession was observed in this region. There is a period of low temperatures during the winter in the bay. In the winter and spring the salinities are quite low. At this time the water at the upper part of the bay is practically fresh. The condition extends somewhat to the outside. On two consecutive years in the late winter and early spring, *Cynoscion nebulosus* was taken in the gulf. The alligator gar was also taken in the gulf during these months. At the same time the fresh-water catfish, *Ictalurus furcatus*, and the river shrimp, *Macrobrachium ohionis*, appeared in the bay. The migration of the latter animal into brackish water has been recorded before by Gunter (1937). These animals are probably more influenced by salinity than temperature. On the other hand *Urophycis floridanus* came from deep water to the bay in winter and the only appearance of *Cynoscion nothus* in the bay was noted in the months of December, January and May. With these two fishes temperature and not salinity was probably the governing factor. Galtsoff (1924) says that mackerel in the Black Sea are very sensitive to temperature, but not to salinity. Ekman (Petterson, 1912) has shown that herring are very sensitive to slight variations in salinity.

During the winter sharks, jackfish and many of the *Carangidae* absented themselves from the bay as well as from that part of the gulf explored by the trawls. In the summer as *Urophycis floridanus*, the fresh-water catfish, and the river shrimp retreat to their respective abodes, the sharks, jacks, threadfins and others return to the shore waters of the gulf. As the summer progresses and the temperatures and salinity of the bay rise some of these fishes move into it and remain there until autumn and the return of low temperatures, whereupon they move back into the gulf and later depart for deep water as the river shrimp, fresh-water cat, and *Urophycis floridanus* return, thus completing a cycle.

SUMMARY

The data for this paper are monthly abundance variations of fishes in trawl catches on the Louisiana coast in Barataria Bay and the Gulf of Mexico, supplemented by general observations and a small number of total length measurements. The time of observation was two and one half years.

There was a sequential, seasonal, yearly variation in numbers of the larger part of the species studied. Knowledge of these variations helps elucidate the life histories of fishes about which something is known, such as the Otolithidae and some Sciaenidae, and gives new light on many hitherto unstudied species, which, however, is fragmentary in some instances.

The data were separated for bay and gulf waters so that movements of the population from one locality to the other could be pictured in some instances. Fishes taken in the bay were smaller than those taken in the gulf. The bay serves as nursery grounds for most of the species studied, although most of them seem to spawn in the open gulf. The young fishes gradually move to the outside as they grow up.

Some fishes are only seasonal residents in the area and the time of their arrivals and departures were rather definite.

A seasonal biological succession of the fish population is briefly described and discussed.

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ECOLOGICAL STUDIES ON THE VERTEBRATE FAUNA OF A 500-ACRE FARM IN KALAMAZOO COUNTY, MICHIGAN

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ECOLOGICAL STUDIES ON THE VERTEBRATE FAUNA OF A 500-ACRE FARM IN KALAMAZOO COUNTY, MICHIGAN

INTRODUCTION

Quantitative research on animal populations has to a considerable extent been restricted to small areas and small animals. Among the best known works of this nature are those of McAtee (1907), Beebe (1916), Wolcott (1918, 1937), Sanders and Shelford (1922), Weese (1924), Blake (1925), Smith (1928), Shackleford (1929), and Townsend (1935). Small controllable populations of invertebrates have served to reveal fundamental principles of population dynamics (Chapman 1928) that may, perhaps, be applicable to all forms; but specific information as to the actual numbers and relationships of vertebrate animals on representative areas is almost wanting.

The study most nearly comparable to what is attempted here is that of Williams (1936), who made a quantitative analysis of a unit of beech-maple forest. The author also investigated the interrelationships of the constituents involved, and discusses the dynamics of the community. Apparently this is the first detailed area study that includes quantitative work on the larger vertebrates.

It is not difficult to account for the small number of investigations that have been made in this field. There are numerous significant obstacles to area studies involving the handling of large populations of birds and mammals. Continuous year-round field work is very desirable if the annual population cycles are to be interpreted, and this is seldom possible. Territory suitable for such work should, for maximum significance, be fairly representative of widespread conditions. It must also be under control as to policies regarding the trapping, shooting, and management of its animal populations. Such areas are not plentiful. In addition to these considerations, the equipment and help necessary for continuous work on a large number of species have not often been available to the student.

The present study results from a cooperative effort on the part of Michigan State College and the Michigan Department of Conservation. Preliminary work was done during the fall, spring, and summer of 1934-35 under a graduate assistantship in zoology at the W. K. Kellogg Bird Sanctuary. From September, 1935 to August, 1937 the study was supported by a half-time research fellowship provided by the Game Division, Department of Conservation. Equipment and expenses also were furnished. Although the interests of the Department of Conservation in these animal populations have principally to do with their value for sport and fur, I have not been limited to a study of game birds and mammals. It has been fully realized that the community of animals associated here must be demonstrated in its entirety before the position of individual species can be appreciated.

Gratitude is here expressed to the Michigan Department of Conservation and in particular to Mr. H. D. Ruhl, in charge of the Game Division, for providing a two-year fellowship and other means of pursuing these studies. Grateful acknowledgement for guidance is made to Dr. M. D. Pirnie, Director of the W. K. Kellogg Bird Sanctuary and chairman of the graduate committee; to Dr. H. T. Darlington of the Botany Department of Michigan State College, who gave needed instruction and criticism in the botanical studies; to Dr. H. R. Hunt, Head, Mr. J. W. Stack, and Mr. Burton T. Ostenson of the Department of Zoology, and to Dean E. A. Bessey of the Graduate School of Michigan State College.

For helpful suggestions and assistance in field work I am indebted to Mr. Farley F. Tubbs, Mr. Paul Hickie, and Dr. G. W. Bradt of the Game Division, Michigan Department of Conservation. Mr. C. M. McCrary, Superintendent of the W. K. Kellogg Farm, cooperated in matters of policy and contributed numerous field observations. Mr. Homer Bradley and Dr. Carl Gower of the W. K. Kellogg Bird Sanctuary gave many valuable field records. This investigation benefited greatly from the services of Mr. Curtis Bartlett who for two winters was transferred from the State Game Farm to assist in the study.

The area upon which the work was done is owned and operated by Michigan State College. Under these circumstances policies have been under reasonable control. Residence at the Kellogg Bird Sanctuary from April, 1935 until August, 1937 has permitted a continuous study. All of my own time was devoted to the work after September, 1935, and a full-time assistant was on the project from October to April during both years.

In scope this study is limited principally to upland forms. Thus no particular investigation has been made of the muskrat, and waterfowl are treated only incidentally. The work has been featured mainly by two activities: the intensive use of box traps during the winter months, and daily field work throughout the year. Both of these methods have been of great value in obtaining the data presented.

The object of this paper is threefold: (1) The area will be analyzed in terms of its physical characteristics and plant habitats. This is necessary to a proper evaluation of the data on animal populations. (2) There is presented a quantitative study of the resident birds and mammals with special reference to the larger species of greater abundance. Where actual population figures are not available the relative numbers of different animals are indicated. (3) The last portion of the work is devoted to a discussion of the interrelationships of these animals with reference to the use of habitats, seasonal and daily times of activity, and to the position of each in the food cycle. In the appendix is given a complete check-list, with scientific names, of all vertebrate species recorded on the area during this work. Hence, for the sake of brevity, vernacular names are usually used in the text.

This is an area study. A unit of the earth's surface, occupied and modified by man, is being described in terms of its plant covering and the animal forms that have found it possible to live here.

THE AREA STUDIED

The territory included in this study is 500 acres in extent and is located in Section 8, Ross Township, Kalamazoo County, Michigan. It includes Wintergreen Lake, which is about 20 acres in area. The southwest corner of Section 8 lies in Gull Lake, the largest body of water in this portion of the state. Along the shore of the lake and separated from the Kellogg Farm by a road is Midland Park. This resort is a collection of cottages, all of which are occupied in summer and where a few people remain in winter. It lies on the flats next to the lake amid a grove of second-growth oaks. On the west the farm is adjacent to two private Gull Lake estates. On the north, east, and south it is bounded by similar farm land.

PHYSIOGRAPHY AND SOILS

The locality treated lies on an extensive outwash plain which was formed in the angle of the Lake Michigan and Saginaw lobes when the ice border was only a few miles from the present site of Gull Lake (Scott, 1921). The region is characterized by pit lakes and kettle holes which, presumably, were formed by the burying of ice blocks which melted and left basins sunk below the surface of the plain. Wintergreen and Gull lakes were probably so formed, as were the five small kettle holes found on the farm.

Wintergreen Lake lies at the 891-foot contour. The highest point on the area is southeast of the sanctuary and is 935 feet above sea level. The sanctuary and that portion of the farm to the west and east are too hilly for cultivation. The level parts of the farm are on the east and north borders. It is in these fields that the cultivated crops are raised.

The soil of the Kellogg Farm is a Bellefontaine sandy loam (Perkins and Tyson, 1926). It is variable as to humus content and in spots is quite sandy. According to the classification of Veatch (1933) it varies locally from first- to third-class farmland. Where the fields are level excellent crops of grain and hay are raised in good seasons. Leverett (1917) gives the principal crops of Kalamazoo County as hay, corn, wheat, oats, potatoes, and rye, and the average value per acre (1917) as $41.72. Perkins and Tyson give the value of Bellefontaine sandy loam as from $30 to $150 per acre, according to location and improvements.

CLIMATE

Kalamazoo County has an average growing season of from 150 to 160 days (Schneider, 1917). The average date of the last killing frost is May 1 to 5. The first killing frost occurs after October 10. Annual precipitation in this portion of the county is usually between 30 and 34 inches (Hill, Riddle, and Elliott, 1930). The mean annual temperature at Kalamazoo is 47.9° F. (Perkins and Tyson, 1926). The summer and winter means are 69.9° F. and 24.9° F., respectively. This project benefited greatly from the presence of a United States Weather Bureau Station (the Gull Lake Station) at the Kellogg Farm. Thus complete weather data were kept on the exact location of the study.

The two seasons of the work were extremely dissimilar. The 1935 growing season was very favorable to all plant life. As a consequence, herbaceous cover was high in the fall and an excellent crop of wild fruits and seeds was produced. The ensuing winter was one of low temperatures and heavy snows which, late in February, reached a depth of 26 inches. Due to the protecting snow very little ice formed on the swales, and soil on the uplands was frozen to a depth of only a few inches.

The summer of 1936 was one of extreme drouth. A new high temperature (108° F.) was recorded for the Gull Lake Station.[1] Crops were much curtailed throughout the region, and fall cover was not so heavy as in the preceding season. The winter that followed was as mild as the winter of 1935-36 had been severe. The ground was bare much of the time, and although temperatures were comparatively high during most of the season, the soil froze to an average depth of nearly a foot.

As the two growing seasons and their effects are important for the purposes of this work, the compiled weather data are for the 2-year period from April 1, 1935 to April 1, 1937. Figure 1 is a climograph comparing mean monthly temperatures and precipitation for the two years beginning April, 1935 and April, 1936. The extent to which the two years differed is readily apparent. Other weather data will be adduced as they are necessary to particular phases of the work.

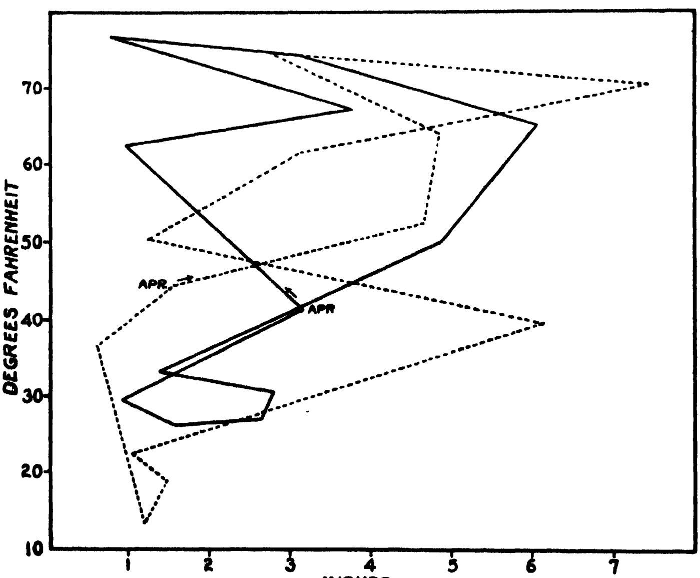

FIG. 1. Climograph showing mean monthly temperatures and precipitation for the two years beginning April, 1935 (dotted line) and April, 1936 (solid line).

[1] Established April, 1929.

RECENT HISTORY

Several farms which then composed this area were purchased by Mr. W. K. Kellogg in 1927, and a year later the entire tract was given to Michigan State College. Eighty acres around Wintergreen Lake were fenced off as the W. K. Kellogg Bird Sanctuary, while the surrounding land became the W. K. Kellogg Farm. The Bird Sanctuary is primarily a waterfowl refuge. In November, at the height of the migration, 3000 ducks of from 10 to 15 species and 500 Canada geese may at one time be found using the lake. From 100 to 300 geese usually remain in the vicinity and feed on the fields in early winter. In the spring it is common for 20 or 30 pairs of mallards and from 10 to 15 pairs of geese to nest around the lake and swales. In summer and winter only a few hundred waterfowl (some captive) occupy the lake and apparently do not greatly affect the resident upland species of the area. The Farm is operated by the college for experimental and demonstration purposes. Corn, wheat, oats, and alfalfa hay are raised; a dairy herd and sheep are kept; and a large poultry plant is operated. In this study no distinction has been made between the territory of the sanctuary and of the farm. Except where the sanctuary is specifically designated, the entire 500 acres is referred to as the Kellogg Farm.

During 1927 extensive plantations of conifers, aggregating about 5000 trees, were set out on the sanctuary and the portions of the farm adjoining to the east and west (fig. 2). Since that time also the natural deciduous brush around the swale and lake margins, which was formerly held back by

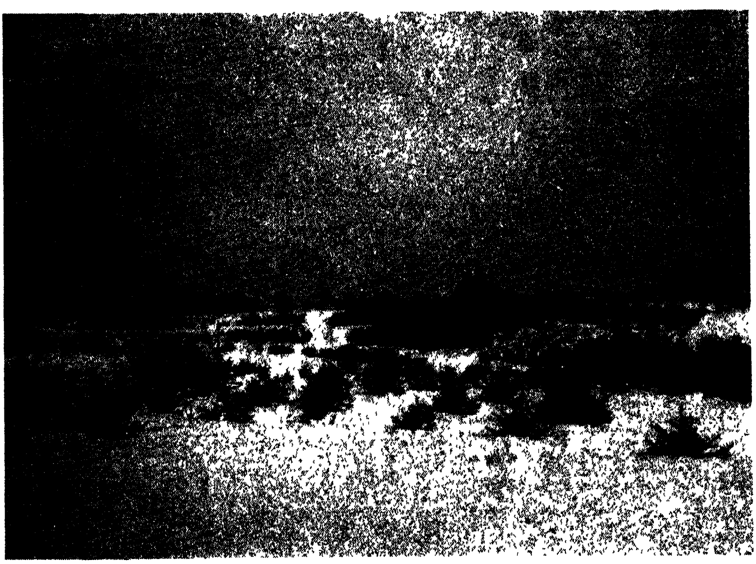

FIG. 2. Coniferous plantations on the W. K. Kellogg Bird Sanctuary in the winter of 1935-36.

grazing, has been allowed to increase into dense coverts (fig. 3). Washes that had started on steep slopes have been filled with stumps. The area apparently supports much more cover now than it did before the sanctuary was established. Otherwise it does not greatly differ from other farm land in the region. Figure 4 shows the distribution of the principal winter cover types during this study.

At the sanctuary the regular winter feeding of small grains has supplemented the natural foods of pheasants and quail. In the winters of 1933 and 1934 standing corn was left in a field at the approximate center of the farm. Chicken house litter containing cracked corn was spread on some fields at two-week intervals through most of every winter. This also has added to the food supply of ground-feeding birds. During this study a few feeding stations were operated for experimental purposes during the winter of 1935-36, and several rye patches also provided food that was available until spring. During the following winter no feeding was done.

The farm area has not been open to general hunting since 1927. The land around Gull Lake for a quarter of a mile back from the shore was closed by an act of the legislature in 1927 and became a sanctuary for all species except rabbits. From 1927 until 1930 intensive "predator control" was practiced at the sanctuary. Steel traps and box traps were constantly set, and all carnivorous mammals and birds were killed as fast as they could be caught. From 1931 to 1935 a small number of skunks, weasels, opossums, hawks, and great horned owls were taken; but the program was not carried on with anything like its former intensity. During this investigation rabbits have been the only

FIG. 3. The west shoreline of Wintergreen Lake showing the dense deciduous brush that has sprung up here since 1927.

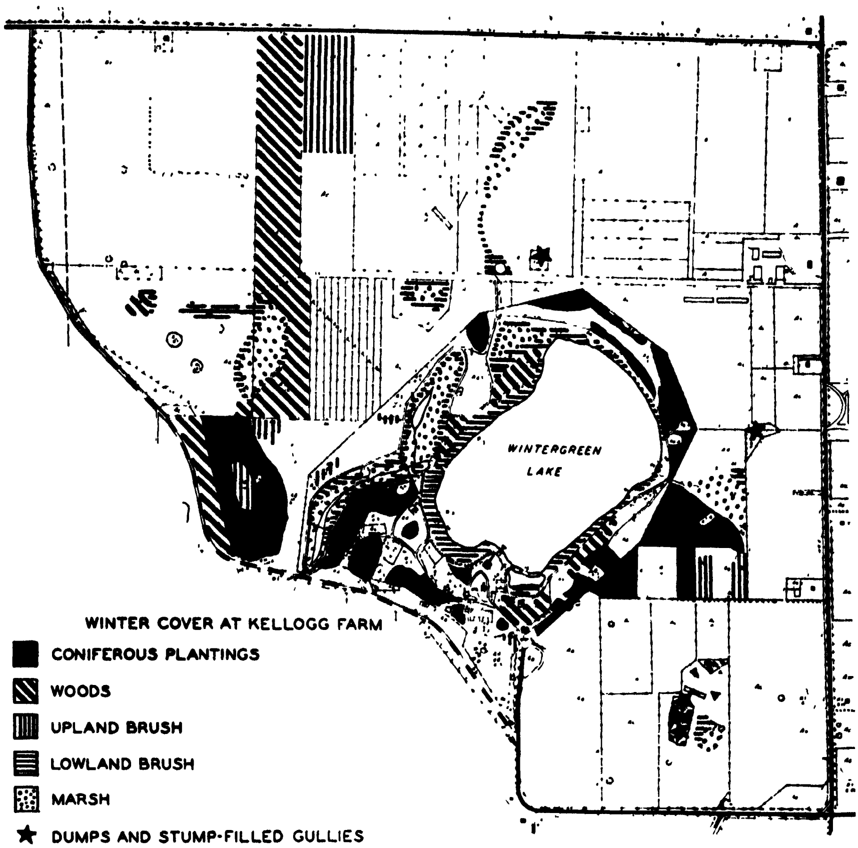

FIG. 4. Distribution of winter cover types on the W. K. Kellogg Farm from 1935 to 1937.

species killed on the area until the population studies were completed in the winter of 1937.

VEGETATION

The Region in General

This portion of Michigan was originally covered by a subclimax forest of oak and hickory. That this is a seral stage dependent upon edaphic conditions is shown by the occupation of the richer and more mesophytic soils by beech and maple, which may be considered the true climax for this region, and which may be expected gradually to replace the more xerophytic oak-hickory stage. As the region has been recently glaciated, the topography is still young. A great variety of conditions exists between the hydrophytic lakes on the one hand and the xerophytic hills on the other. As the hills are eroded and the lakes are filled the mesophytic areas increase (Cowles, 1901) and may, under natural conditions, be expected eventually to characterize the region.

The nature of the original forest was described by Durant (1880) and by Thomas who, writing in 1869 says, "—the surface is rolling—and is composed principally of oak openings with some beech and maple skirting the river and some of the creeks."[2] As the Kellogg Farm supports no beech-maple the entire area may be considered developmental from the standpoint of succession. The hydrosere[3] is represented in the kettle holes and Wintergreen Lake, while the stages of the xerosere may be found on the upland. As the latter are artificial in origin (due to the activities of man) they are classed here as belonging to a secondary succession in contradistinction to the natural, or primary, hydrosere (Weaver and Clements, 1929). The sere is used as a convenient vehicle for the presentation of habitat data. The natural, or prisere, is given first, with later a discussion of the main type of secondary succession found here (succession from plowed ground). The artificial plantings are treated under the heading "Artificial cover types."

Habitat Types on Kellogg Farm

In this work the term "predominant" has been used to indicate animals active throughout the year. From the same standpoint all others are "seasonals" (Smith, 1928). In designating an animal species as "characteristic" of a given habitat it is implied that the species has shown a marked predilection for that type of environment. Species may not be listed as characteristic of any habitat on the area either because observations are too few to justify it, or because the animal has made extensive use of several habitats. Thus such important animals as the cottontail rabbit, skunk, and pheasant cannot be said to belong to any particular habitat, considering their behavior during the entire year.

Primary Succession, a Hydrosere

Open Water Habitat.—This habitat is present only in Wintergreen Lake. It is not treated in this study and is mentioned only as the initial stage in the hydrosere. A list of the fishes and amphibia found in the lake is given in the appendix (see check-list of vertebrates for the area, p. 430).

Marsh Habitat.—The total area of this habitat is approximately ten acres. It is divided into six principal units, the largest of which is the long swale along the outlet of Wintergreen Lake on the sanctuary. Although the water level here is variable, it does not normally fluctuate to the extent that it does in undrained marshes. The level of the lake itself must drop several feet before these swales become dry. The undrained kettle holes on the area (four in number) are, typically, small units of marsh surrounded by a narrow belt of swale brush. These two habitats are clearly defined and hence are discussed separately. Swales are much influenced by the amount of rainfall in any par-

[2] Kalamazoo River.

[3] The parts of this area that are now covered by oak woods have, since the advent of man, never supported any other type of cover. Hence these areas may be said to have developed by natural stages with no artificial interference. This type of natural sere is designated a primary succession or prisere. The lowest stage of this natural succession is open water; hence it is a hydrosere. The alternative condition is succession starting from bare soil or rock. In such a case the unit succession is termed a xerosere. All the stages of a natural xerosere do not occur on this area.

ticular season. During an exceptionally dry year the buttonbush of the brushy margins actively invades the marsh. A correspondingly wet year retards this invasion.

The marsh habitat varies considerably with the season and with the extent to which the deposition of humus in any particular swale has tended to fill it in and to render the area more xeric.

In the deepest parts of the swales the water is several feet in depth and the bottom is soft partially-decayed humus. Here the most characteristic hydrophyte is *Nymphozanthus advenus* (yellow pond lily). *Polygonum coccineum* (water smartweed) is often found in pure growths, particularly along edges where the rhizomes extend beneath the soil and connect with sprouts on the bank. In May of 1935 the water of the swales was in many places completely covered with the small thalli of the floating liverwort *Ricciocarpos natans.* In this season duckweeds were very scarce. In the 1936 season little Ricciocarpos was present, but the duckweeds *Spirodela polyrhiza* and *Lemna minor* occurred in small quantities. Waterfowl fed upon all these natant plants.

In shallow parts of the water a solid stand of *Typha latifolia* (cat-tail) sometimes occurs to the exclusion of all other species. This plant is found more sparingly in the swales that become dry in late summer. Here *Carex* sp. (sedge), *Phalaris arundinacea* (reed canary grass), *Calamagrostis canadensis* (blue-joint grass), and *Polygonum sagittatum* (arrow-leaved tear-thumb) are more common. In one swale *Eleocharis palustris* (spike rush) occurs. Other common plants of this habitat are *Asclepias incarnata* (swamp milkweed), *Rumex verticillatus* (swamp dock), and in shaded places *Impatiens biflora* (jewel weed).

A small swale on the east side of the farm has been drained by a ditch leading into the lake. There is no standing water here at any season and conditions are dryer than in the other marsh areas. A very few square feet of moist ground at the center are occupied by *Polygonum hydropiper* (water pepper) and around it an extensive solid growth of *Polygonum sagittatum* extends out to the edges of the former marsh. We find a similar condition in the dryer portions of other kettle holes. The above plants, as well as *Polygonum persicaria* (lady's thumb), *Polygonum pennsylvanicum* (Pennsylvania smartweed), *Polygonum orientale* (prince's feather), and *Polygonum acre* (smartweed) are to be found around the lake and the various swales where moisture conditions are favorable. Many of these species produce winter foods of value to seed-eating birds.

The following animals may be considered characteristic of the marsh habitat on this area:

Amphibians

Pseudacris triseriata (Swamp tree frog)
Hyla crucifer (Spring peeper)
Rana pipiens (Leopard frog)

Reptiles

Emys blandingii (Blanding turtle)

Birds

Agelius p. phoenicus (Redwing blackbird)

Botaurus lentiginosus (American bittern)

Porzana carolina (Sora rail)

Anas p. platyrhynchos (Mallard duck)

Mammals

Ondatra z. zibethica (Muskrat).

All of these amphibians are inactive in winter. The birds also are absent at this season. The muskrat alone is active throughout the year and thus is the only predominant animal of this habitat.

Lowland Brush Habitat.—The irregularity of this habitat and the fact that it occurs in small units render its total area difficult to compute. It is probably near eight acres. Its spotty distribution and the fact that it often is present in long narrow strips make it of more importance to animal species than would be inferred from its actual area. This habitat borders most of the shore line of the lake and forms a brushy margin around the greater portion of the swales.

The lowland brush habitat may be divided into three principal types. *Cephalanthus occidentalis* (buttonbush) is a well-defined type which exists in comparatively pure stands in the wetter portions of the habitat. Exceptionally wet weather retards its invasion of the water but does not kill it out. In dry years it makes rapid progress.

A second type of swale brush, usually found outside (away from the water) and on dryer soil than the buttonbush, is characterized by a mixture of *Cornus candidissima* (gray dogwood), *Cornus amomum* (silky dogwood), *Cornus stolonifera* (red-osier dogwood), *Sambucus canadensis* (black elder), and various less plentiful shrubs such as *Rosa* sp. (bush rose), *Viburnum lentago* (nannyberry), *Amelanchier canadensis* (service berry), and others. The mixed shrubs constitute the most exensive swale brush type. It is variable, often with one of the constituents, such as gray dogwood, red-osier dogwood, or elder, forming a pure stand locally.

A third distinct type of lowland brush is willow. In spots of low sandy soil that are not too wet *Salix longifolia* (sandbar willow) flourishes. The stems are typically from eight to ten feet in height and grow in close, pure stands. The best example of this growth is in the large kettle hole on the west side of the farm. In much the same type of situation an active growth of *Populus tremuloides* (quaking aspen) is sometimes found. The young shoots are often mixed with the shrubs, and in dryer places the larger trees may assume dominance.

There are numerous other plants that are typically associated with the above brusy types. *Salix bebbiana* (Bebb willow), *Salix petiolaris,* and *Salix*

FIG. 5. An undrained kettle hole on the Kellogg Farm showing willow brush in the foreground, an extensive growth of reed canary grass in the marsh, and the upland woods in the background.

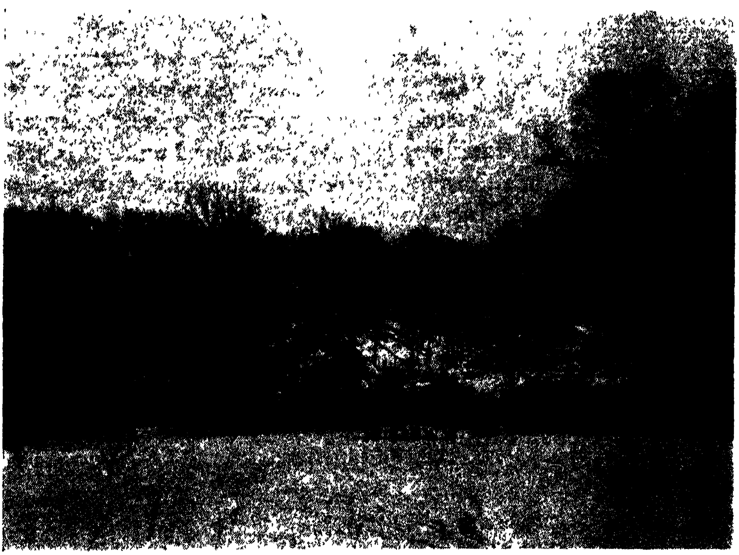

FIG. 6. The appearance in winter of the same kettle hole shown in fig. 5.

discolor (pussy willow) are common as shrubs, while *Salix nigra* (black willow) and *Salix amygdaloides* (peach-leaved willow) become large trees and occur as individuals here and there along the swale and lake margins. In openings among the larger shrubs *Spiraea alba* (meadow sweet), *Rubus idaeus strigosus* (red raspberry) and such herbaceous forms as *Urtica gracilis* (nettle), *Thelypteris palustris* (swamp fern), and *Phytolacca americana* (pokeberry) are common. *Cuscuta pentagona* (dodder) and *Polygonum scandens* (climbing false buckwheat) are often found vining through the marsh plants or over the buttonbush respectively.

This habitat forms the most important natural winter cover on the area. Although many animals live in it, few are restricted to it. The greatest discrimination in favor of the swale brush is shown by certain species of nesting birds.

Birds

Dendroica a. aestiva (Yellow warbler)
*Empidonax t. traill*i (Alder flycatcher)
Dumtella carolinensis (Catbird)
Melospiza m. melodia (Eastern song sparrow)

Mammals

Zapus h. hudsonius (Meadow jumping mouse)
Peromyscus leucopus noveboracensis (Northern white-footed mouse)
Blarina b. brevicauda (Short-tailed shrew)

Of the above animals the white-footed mouse and the short-tailed shrew are predominants.

Lowland Woods Habitat.—Lowland woods is the least extensive of the major habitats found on the Kellogg Farm. It is present only as a trace that tends to mix with the upland woods on low ground. Around the large kettle hole at the south end of the farm woods is the best-defined unit. It is probably less than an acre in extent, although mixture with the upland type makes difficult the setting of limits. North of the outlet of Wintergreen Lake, between the lake and the swale, the presence of considerable red maple gives the growth a low woods character, although the upland oaks are numerous here also.

The most definitive species of this habitat are *Acer rubrum* (red maple), *Ulmus americana* (American elm), and *Fraxinus americana* (white ash). Associated with these trees *Laportea canadensis* (wood nettle), *Impatiens biflora* (jewel weed), and *Parthenocissus quinquefolia* (Virginia creeper) are common. Due to its limited extent no vertebrate animals in particular can be said to characterize the habitat on this area.

Upland Woods Habitat.—On the farm and sanctuary there are approximately 30 acres of oak woodland, which is divided into four principal areas. The largest of these is in the northwest quarter of the farm and is a little under 20 acres in extent. Another plot of woodland lies on the southwest

boundary. The latter is all second growth, having been completely cut off within recent times. Only about two acres of this is within the area studied. The trees are from six to ten inches in diameter, and there is a considerable admixture of *Populus grandidentata* (large-tooth aspen). This species, as would be expected, is fast giving way to the oaks. The oldest oak areas are on the sanctuary. To the southeast of Wintergreen Lake the growth lies in a divided strip of less than three acres. On the northwest side of the lake the "sanctuary woods" forms a unit of about two acres. Cutting has not been extensive in these areas and many of the trees (18 to 24 inches in diameter) may be considered a part of the original forest.

As before stated the upland oak woods represents the most advanced seral stage present on this area. The largest woodlot of twenty acres functions most characteristically on account of its size and is referred to in this description.

The trees most typical of the habitat are oak and hickory. Of the three species of oak present *Quercus velutina* (black oak) is the most abundant, with *Quercus borealis maxima* (red oak) second in importance. *Quercus alba* (white oak) is the least common of the three. Among the oaks is to be found a fairly constant mixture of *Carya glabra* (pignut hickory), *Prunus serotina* (wild black cherry), *Acer rubrum* (red maple), and, in spots, *Fraxinus americana* (white ash). Red maple and ash are more characteristic of the low woodland habitat but often occur as secondary species in the upland oak woods of this region, becoming more numerous in locations of greater moisture.

A few of the oaks are from 18 to 24 inches in diameter. These probably were young trees when the first cutting was done in this locality. Stumps in varying stages of decay show that selective cutting has very probably been going on for fifty years or more. Around the larger and older stumps will sometimes be found a stand of young oaks nearly uniform in size. All the dead, hollow, and misshapen trees have been removed recently for firewood. Few ground logs are present and these are small.

The woods is naturally open in character and in spots a few individuals of *Cornus florida* (flowering dogwood) or *Malus coronaria* (wild crab) occur, with here and there a fairly dense growth of *Sassafras officinale* (sassafras). In areas of increased insolation a sparse tangle of *Rubus allegheniensis* (blackberry) and *Rubus idaeus strigosus* (red raspberry) is produced. Individuals of *Ribes floridum* (wild black currant), *Ribes cynosbati* (wild gooseberry) and a bush rose, *Rosa* sp., are to be found at intervals in the stand.

Throughout most of this habitat there occurs a sparse growth of *Poa pratensis* (Kentucky bluegrass), *Poa compressa* (Canada bluegrass), or a fine grass-like sedge, *Carex* sp. A moss, *Polytrichum* sp., is common in the more shaded portions.

Among the characteristic herbs of the woods floor are *Claytonia virginica* (spring beauty), *Hepatica americana* (hepatica), *Viola cucullata* (blue violet), *Erythronium albidum* (white dog's-tooth violet), *Geranium maculatum* (wild geranium), *Polygonatum pubescens* (Solomon's seal), *Podophyllum peltatum* (May apple), *Smilacina racemosa* (false Solomon's seal), and, in the more sunlit grassy portions, *Antennaria canadensis* (everlasting), and *Galium* sp. (bedstraw). Claytonia, Erythronium, and Podophyllum, in particular, tend to form noticeable vernal socies.[4]

On the whole, most of the woodland gives evidence of being well-drained and in spots rather dry, as evidenced by the presence of such plants as *Poa compressa*, Antennaria, and Sassafras. Ecotones between the woodland and other types of habitat are in most places well defined.

The following vertebrates occur typically in the oak upland habitat:

Amphibians
- *Hyla v. versicolor* (Tree frog)

Birds
- *Buteo b. borealis* (Red-tailed hawk)
- *Corvus b. brachyrhynchos* (Eastern crow)
- *Myiarchus crinitis boreus* (Northern crested flycatcher)
- *Vireo olivaceus* (Red-eyed vireo)

Mammals
- *Sciurus niger rufiventer* (Fox squirrel)
- *Glaucomys v. volans* (Flying squirrel)
- *Tamias striatus lysteri* (Eastern chipmunk)
- *Peromyscus leucopus noveboracensis* (Northern white-footed mouse)

Of the above vertebrates the fox squirrel, white-footed mouse, and crow may be designated as predominants. All others of the indicated species are seasonals. The tree frog and chipmunk are inactive in winter, while the red-tailed hawk, crested flycatcher, and red-eyed vireo are absent due to migration.

Secondary Succession, a Xerosere

Plowed Ground.—As this is the initial stage in an important man-made succession, it is here ranked as a habitat in the sere. No discussion is needed.

Annual Weed and Cropland Habitat.—The acreage planted to annual crops varies somewhat from year to year, but averages about 60. Slightly more than one-half the farm (277 acres) has been cultivated, but much of this is usually kept in pasture or hayfields. As before mentioned, the cultivated fields lie on the east and north borders of the farm.

A cornfield most typically represents the annual weed stage in the succession from plowed ground and may be taken as a good example for description. The plants that first appear on newly broken ground are such annuals as

[4] The developmental equivalent of the society (Weaver and Clements, 1929). In this case a seasonal socies.

Ambrosia elatior (ragweed), *Amaranthus graecizans* (tumbling pigweed), *Chenopodium album* (lamb's quarters), and *Amaranthus retroflexus* (red-root). Grasses characteristic of the first season's growth are *Panicum capillare* (panic grass), *Setaria lutescens* (yellow foxtail), *Setaria viridis* (green foxtail), and *Eragrostis cilianensis* (stink grass). *Digitaria sanguinalis* and *Digitaria ischaemum* (crab grass) are often found on cultivated ground and in low fields *Echinochloa crusgalli* (barnyard grass) is apt to be common. Practically all of these ruderals produce fruits that are used as food by winter birds, thus making weed and croplands the most productive habitat from this standpoint.

It is commonly observed that the annual weed stage follows the breaking of the ground regardless of what the existing plant cover may be. It has been demonstrated that the seeds of these annuals are present in practically all soils, only awaiting favorable conditions to germinate. An experiment initiated by Dr. W. J. Beal in 1879 indicates that the seeds of some species may remain buried and viable for more than 50 years (Darlington, 1931). In Woburn barley soil Brenchley and Warington (1930) found more than 150 seeds of *Chenopodium album* per eight and two-thirds square feet. Chippindale and Milton (1934) demonstrated the seeds of annuals in the soil of permanent pastures that had not been cultivated for many years. That this phenomenon has an important influence upon animal life, particularly in winter, cannot be doubted.

Only one vertebrate species appears to make cultivated fields its permanent habitat. It is active during the entire year.

Peromyscus maniculatus bairdii (Prairie deer mouse)

Grassland Habitat.—The extent of this habitat can not be accurately stated. It increases as cultivated fields are allowed to revert temporarily to grassland pastures and diminishes as these are plowed for cultivated crops. Grassland is extensive and interdigitates with all the other habitats on the area. Probably one-fifth of the farm usually supports such cover.

The grassland habitat is very reflective of edaphic conditions. The better soils in this vicinity support a rank growth of *Poa pratensis* (Kentucky bluegrass). The dry, less fertile uplands are extensively occupied by *Poa compressa* (Canada bluegrass). Other grasses occurring commonly are *Dactylis glomerata* (orchard grass), *Cenchrus pauciflorus* (field sandbur), *Phleum pratense* (timothy), *Bromus tectorum* (downy brome grass), and several cultivated grasses that have been used for experimental purposes at the Kellogg Farm.

Some of the more common weeds found growing in grasslands are *Verbascum thapsus* (mullein), *Cirsium lanceolatum* (bull thistle), *Erigeron canadensis* (horse-weed), *Erigeron annuus* (daisy fleabane), *Plantago lanceolata* (buckhorn), and *Rumex acetosella* (field sorrel).

On the sanctuary ten years of constant pasturing by geese has practically eliminated the grass that formerly grew on the open slopes. As a consequence, these areas are almost entirely occupied by *Plantago lanceolata*, *Potentilla canadensis* (cinquefoil), *Hypericum perforatum* (Saint John's wort), *Erigeron annuus*, *Erigeron canadensis*, and a few other species of similar habit. The more dry and sterile soils where erosion has begun are in spots covered principally by the moss *Ceratodon purpureus*. Of the above species of plants *Erigeron annuus*, *Hypericum perforatum*, and *Erigeron canadensis* form well-defined seasonal socies in the order named from June until August.

The following birds and mammals characterize the vertebrate life of the habitat:

Birds
- *Otocoris alpestris praticola* (Prairie horned lark)
- *Ammodramus savannarum australis* (Eastern grasshopper sparrow)
- *Pooecetes g. gramineus* (Eastern vesper sparrow)
- *Spizella p. pusilla* (Field sparrow)

Mammals
- *Peromyscus maniculatus bairdii* (Prairie deer mouse)
- *Microtus p. pennsylvanicus* (Eastern meadow mouse)
- *Citellus t. tridecemlineatus* (Thirteen-lined spermophile)

Of the above-named species all of the birds are absent part of the year due to migration. The spermophile hibernates. Thus the two species of mice are the only predominants.

Upland Brush Habitat.—The largest area of upland brush is a cut-over woodlot of seven acres which lies next to the woods on the north side of the farm. Other small or very sparse units are scattered here and there over the farm and sanctuary aggregating, perhaps, three acres. The habitat is one of the least extensive on the area.

Several species of woody plants characterize the upland brush habitat as it occurs on this area. In the well-drained sandy soil of the vicinity *Sassafras officinale* is almost sure to be present. *Rubus allegheniensis* (blackberry), *Rubus occidentalis* (black raspberry), *Rubus idaeus strigosus* (red raspberry), and *Rosa* sp. (rose) commonly form a thick tangle. One of the most typical trees of this type of cover is *Crataegus* sp. (hawthorn), and oak brush is likely to be an early invader. Over these trees, brush heaps, and through the briars a heavy growth of *Vitis vulpina* (wild grape) is frequently found. *Rhus copallina* (dwarf sumach) is often very common in such habitats.

In the seven-acre brush area on the farm the most common herbaceous species are *Poa pratensis*, *Pteridium latiusculum* (bracken fern), *Monarda fistulosa* (wild bergamot), and *Solidago* sp. (goldenrod). *Asclepias syriaca* (common milkweed) also occurs here.

A distinct type of upland brush in this region is *Rhus typhina* (staghorn

FIG. 7. The annual weed and crop-land habitat as illustrated by a cornfield in the fall of 1936.

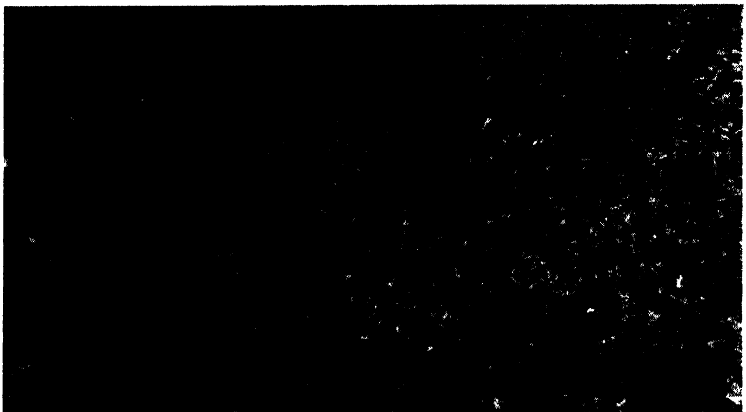

FIG. 8. *Chenopodium album* (lamb's quarters) growing on cultivated ground. This plant produces quantities of food for seed-eating animals in winter.

sumach) which grows on grassy hillsides where insolation is high and conditions tend to be xeric. This species grows in pure close stands. It is seldom found mixed with other woody plants and is a poor type of cover for animal life.

The northern white-footed mouse *(Peromyscus leucopus noveboracensis)* is perhaps the most characteristic animal of this habitat. It is active throughout the year.

Upland Woods Habitat.—Invasion of the upland brush by oak and hickory eventually results in its displacement by the upland oak woods. This habitat has already been described.

Artificial cover types

Coniferous Plantations.—In 1927, when the area was purchased, large plantings of conifers were made on the 80 acres of the sanctuary and the hilly parts of the farm adjoining to the east and to the west. The stands vary in extent from a few scattered trees to five acres of massed pines. The species most commonly used were Scotch pine *(Pinus sylvestris)*, red pine *(Pinus resinosa)*, white pine *(Pinus strobus)*, and white spruce *(Picea canadensis)*. Smaller numbers of Austrian pine *(Pinus nigra austriaca)*, western yellow pine *(Pinus ponderosa)*, and Norway spruce *(Picea abies)* have also been used. On the sanctuary small clumps of white cedar *(Thuja occidentalis)* and ground juniper *(Juniperus communis depressa) were planted.* Approximately 20 acres have been planted to conifers and the plantings are scattered over an area of about 100 acres, extending from west to east across the farm and including the sanctuary.

The coniferous plantations were made, for the most part, in grassland, and this cover type is present wherever the pines are spaced far enough apart for any other plants to grow. The most characteristic animal of the smaller spruces and junipers is, perhaps, the chipping sparrow *(Spizella p. passerina)*. The large trees are a favorite nesting site of the eastern mourning dove *(Zenaidura macroura carolinensis)* and the eastern robin *(Turdus m. migratorius)*. The white-footed mouse is also commonly found here.

Deciduous Plantations.—In the summer of 1935 a study was made of cover distribution on the Kellogg Farm by the Michigan Department of Conservation. Banks, gullies, edges, and corners of fields over the farm were fenced off and planted to oversized nursery stock. Most of the species used were food-bearing shrubs. Some of the genera most commonly represented were Cornus, Viburnum, Berberis, Amorpha, Lonicera, Symphoricarpos, Ligustrum, Rosa, Ptelea, Morus, and Eleagnus.

During the severe drouth of the 1936 growing season these plantings made poor progress and many of the shrubs died. For the period of this study the planted areas have not been an important habitat type and hence can be

passed over with little comment. These shrubs are ideally situated to improve the cover distribution of the farm, but their growth to date has not been sufficient for them to serve an important function in this respect.

SEASONAL CHANGES

In order to convey a clearer impression of the changes which this animal environment undergoes it will be well to review briefly the main differences in its seasonal aspects.

In summer the area is characterized by very dense cover everywhere. The vigorous plant growth of this season provides a plentiful basic food supply for herbivores and through them, all other species. Insects, frogs, and other forms are abundant, and the young of all species are present as food and as the consumers of food. The capacity of the area for supporting life reaches its height in summer. Although the numbers of animals present and their activity are at a maximum, the observation of terrestrial forms is extremely difficult due to the sheltering greenery that is everywhere.

In the autumnal aspect the green of summer is gone. Killing frosts have reduced herbaceous vegetation, though it is still important as cover. In wooded areas the ground is thickly layered with leaves. The chief characteristic of autumn, however, is the tremendous abundance of mast, fruits, and seeds. All this does not remain to support resident winter populations, since large flocks of migrant birds demand a large food supply. The foods that are present in fall depend to some extent upon the nature of the growing season that went before. However, abundance is the rule despite the fact that insects are rapidly disappearing at this season and many of the "cold bloods" are becoming inactive.

In winter a variety of conditions may exist; but there is usually considerable snow on the ground in this region, which effects material changes in ground cover. Under deep snow herbaceous vegetation becomes of very minor importance. Thick brush, conifers, or holes in the ground become the retreat of species that need such protection. Large open areas that supported abundant life in summer appear to be deserted in winter. Animal populations and food supplies diminish to their lowest point late in the season, although the early melting of snows may increase the availability of foods to some extent. Winter is the season of the progressive destruction of what the summer has produced.

In early spring vegetation has reached its lowest point, although the disappearance of the snow renders available as cover the more enduring herbaceous plants of the summer before. This absence of snow also makes possible the gleaning of the last remnants of the fall abundance of fruits and seeds. As new plants begin to grow, insect life awakens, and many species start to breed. Gradually, with the advent of migrant birds and the increasing vegetation, the activity of summer is resumed.

ANIMAL LIFE OF THE AREA

The widely varying habitats of this portion of Michigan support correspondingly different animal populations. The biota of a creek bottom will be found to differ materially from that of an upland farm in an adjacent section of land. Although the region as a whole presents a heterogeneous pattern of distinct communities, nearly any 10-mile square will be found to contain a large portion of the vertebrate species occurring anywhere in southern Michigan.

In the appendix is given a list of all the vertebrates recorded on the Kellogg Farm during three years. Alone, this check-list would present a very poor picture of the associated species living here. Several of the animals listed have been recorded only once on this area, although they may be common within a few miles. In neighboring creek bottoms, in particular, the fauna contains many species not found on the Kellogg Farm. In a glance at the list of Amphibia a conspicuous lack of salamanders is noticed. Only one salamander *(Ambystoma maculatum)* has been recorded in three years, although a particular effort was made to find more. There is only one record of the pickerel frog, which is common around near-by spring-fed streams. The green frog and wood frog are present in only small numbers, while the leopard frog is very plentiful. The Fowler toad and the American toad are both common. Snakes are not numerous on the farm, the ribbon snake probably being most frequently seen. Turtles are abundant both in the lake and in the swales. The list of birds for the area is very complete in the case of waterfowl and sparrows, but is limited for warblers. The sparrow hawk is not often seen, though it is common a few miles away. The swamp sparrow, Henslow sparrow, indigo bunting, and short-billed marsh wren are seldom observed on the area, although they may easily be found in certain habitats not far distant. A red squirrel has been found on the farm only once; yet two miles to the east it is common in the tamaracks around Augusta Creek. The only record for a fox[5] was in February, 1937, when one animal left tracks on the area for several nights. No star-nosed mole has been captured during this work, but one was taken here in 1933. Bats have been seen at the sanctuary but none collected. Only two pine mice and one least shrew have been taken in three years. The animals of infrequent occurrence are probably of little significance in the bionomics of the area, and they need be little more than mentioned here.

POPULATION STUDIES ON CERTAIN ANIMALS

In the following pages will be given the results of an attempt to ascertain the numbers present of the species of resident upland birds and mammals. The work has been most nearly complete for the cottontail, fox squirrel, skunk, opossum, pheasant, and quail. Data on hawks and owls are restricted to field observations.

[5] The red fox recorded in the check list was identified on the basis of these tracks. There was little doubt that the animal was this species as the gray fox is very rare in this region.

METHODS

The census methods used on the larger mammals varied somewhat and are discussed under the several species. In general, trapping and marking have constituted a basis for the work. A line of from 20 to 70 box traps (fig. 9)

FIG. 9. Box traps covered with third-inch-mesh hardware cloth were used in taking the larger mammals.

was run from October to April during both winters of the study. Figures 10 and 11 give the distribution of traps during the two winter seasons. Traps were placed, for the most part, in brush cover, as this was particularly desirable from the standpoint of the rabbit study. The baits used were an ear of corn and half a chicken. The corn attracted rabbits, squirrels, pheasants, and quail. The chicken was an efficient bait for skunks, opossums, and house cats. Both baits usually were used in each trap set.

Pheasants and quail were censused by traversing the area with as many men and dogs as were available. The numbers of men used varied from 5 to 12, and there were usually from 1 to 4 dogs. Every part of the farm was included, the more dense cover being worked most intensively. Birds flushed were marked down and duplicates avoided as much as possible. This method

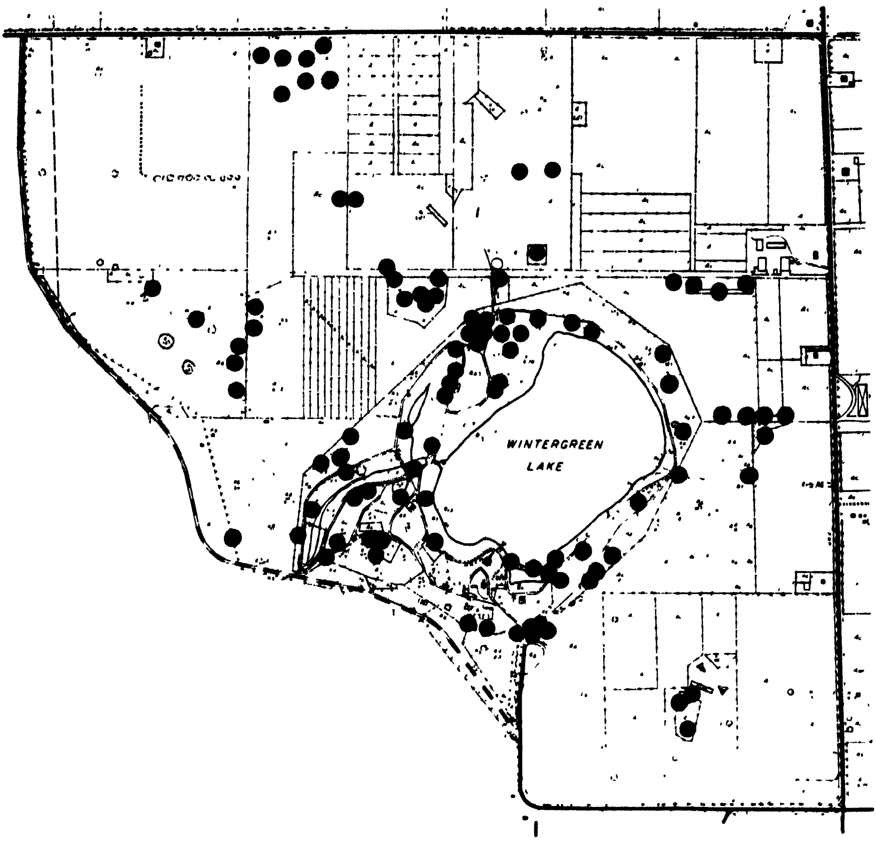

FIG. 10. Distribution of box traps during the winter of 1935-36.

was by no means perfect; but a repetition of such censuses, together with regular field work and the results of trapping and banding, appear to have given a fairly accurate indication of the number of birds on the area.

The habitat preferences and relative abundance of mice and shrews were ascertained by operating a line of 200 ordinary mouse traps during fall, winter, and spring, as time allowed. The traps were set three feet apart and baited with peanut butter. The work of Townsend (1935) indicated that peanut bait would be acceptable to all of the species present here. Field observations on tracks, burrows, and nests also were useful indices of the abundance of small mammals. The population numbers of these animals are indicated only relatively.

In giving numerical values to animal populations it is necessary to state the time of year for which a census is calculated. Populations are being continuously augmented in the spring and summer breeding season and steadily reduced in winter. Nearly all of the figures for the area studied represent

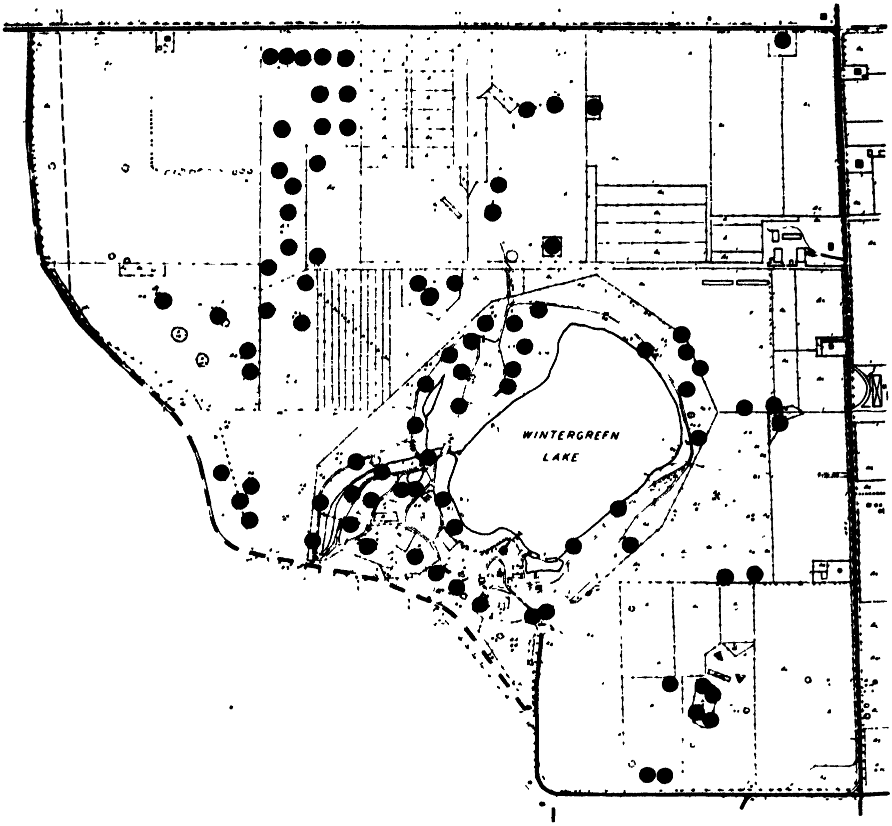

FIG. 11. Distribution of box traps during the winter of 1936-37.

the winter season. For most species it has not been possible to be more specific than this, but for rabbits a definite date is given. Population figures are, of course, only approximate.

LARGER MAMMALS AND BIRDS

Cottontail Rabbit

The section of land here treated has been known for many years as good hunting territory for cottontails. The increase in the natural coverts since 1927 and the planted conifers appear to have made the area even more favorable to this species.

Technique.—After preliminary experiments with apples, oatmeal, wheat, and scratch feed, it was found that the best bait for rabbits was an ear of corn. The chief advantage of this bait was that it was not carried away by mice nor easily covered up by snow. Intensive rabbit trapping was started on January 1, 1936. At this time it was apparent that rabbits had gathered into cover patches all over the farm. Hence traps were confined, for the most part, to these locations (fig. 10). As tracks were nearly absent from open

fields and less than 30 traps were available at this time, it was necessary to use the latter as effectively as possible. Throughout these studies traps have been placed where signs showed rabbits to be most plentiful. As the trapping was confined chiefly to late fall and winter, the greater part of it was done in deciduous brush, coniferous plantations, planted washes, and dumps, where rabbits were most numerous at this season. Table 1 gives the summarized rabbit trapping data for the entire study.

TABLE 1. SUMMARIZED RABBIT TRAPPING

Period	Trap nights	Individuals handled	Repeats	Total catch
December, January, February, March, 1935-36	3,342	70	366	436
October 31 - December 17, 1936	2,045	102*	96	187
January, February, March, 1937	5,289	24	94	106
Totals	10,676	182**	556	729

*Including repeats on some rabbits marked in former trapping periods.
**The rabbits marked formed a numerical series from 1 to 181. There was one uncorrected duplication that makes the total number of individuals 182. Several rabbits were taken by methods other than trapping and so are not included in the total catch by trapping; they are, however, represented here in the total of marked rabbits.

In this study rabbits were marked by tattooing a number on the inside surface of the right ear. The rabbit was placed in a small cloth bag and the ear slipped out through a hole. A sharp pen was dipped in black carbon ink and the number stippled in by puncturing the skin. Such numbers were permanent and easily read.

Census of December, 1935.—In 1935 rabbit shooting began at the sanctuary and farm on December 3. During the month of December a total of 154 rabbits were killed on the 500 acres. In the trapping period from January 1 to March 31 individual rabbits taken and marked numbered 63. In addition to these, 11 more unmarked rabbits were recorded as mortalities.[6] Hence 228 individual rabbits were handled. If there was no general movement of rabbits onto or from the area during the period of the shooting and the period of trapping, the number of animals given represents a minimum population figure. For those who consider "hunting pressure" as a force tending to drive rabbits off the farm, it is to be pointed out that most of the surrounding land was also being hunted. On the other hand, for those who may consider the hunting on the farm as tending to evacuate favorable habitats which might be filled by an influx from outside, it must be remembered that an apparently similar reduction of the population density was taking place outside the area. Range records show that there is a marked tendency for individuals to remain in a given locality when the ground is covered by snow in the winter. There is no indication of a trend of movement onto or from the farm. There is, however, no actual proof that such a movement did not take place, and this is a possible source of error that may be evaluated in a number of different ways.

[6] Three additional mortalities in which the ears were eaten by predators were probably marked animals (from circumstances). They are not added here as it is likely that they are already included in the total of 63. There is a possible error of three in the total of handled rabbits.

TABLE 2. RABBIT TRAPPING BY MONTHS; WINTER, 1935-36

	December*	January	February	March
New rabbits caught	3	37	15	8
Total individuals handled (old and new)	3	39	44	27
Total repeats	0	85	197	84
Trap nights	12	608	1,064	1,658

Individuals caught on Farm	63
Individuals caught on Kellogg Eestate	7
Total rabbits marked to April	70

*Only three days' trapping included

If it is postulated that rabbits were not driven off the farm by shooting and did not gravitate to the area to occupy desirable habitats in which the population was reduced, the main question regarding this type of census is whether or not a large percentage of the rabbit population was handled. Table 2 shows that during January, plus three days in December, 40 rabbits were marked. In February the number of new rabbits caught declined to 15. In March the number of new rabbits dropped to eight. A progressive decline in the number of new unmarked rabbits caught is to be expected as more and more of the population are marked. The fact that only eight new animals were taken during March indicates that the trapping job had accounted for a large portion of the rabbits on the farm. As shown by fig. 12, however, the efficiency of traps dropped significantly during March, and this fact must be considered in evaluating the results. It is not possible to say how many unmarked rabbits remained after April 1. It seems probable, however, in the light of subsequent work, that if this number were known, our minimum population figure of 228 would not be increased enough to alter greatly conclusions as to the status of the species on this area. Probably a more reliable basis for judging the census is obtained from the results of an entirely different type of population count taken during the following winter season.

Census of December, 1936.—In the fall of 1936 facilities were at hand for a census employing the "banding returns" principle which Lincoln (1930) suggested could be used in calculating the abundance of American waterfowl. The plan was to mark as many rabbits as possible over as short a period as possible. Immediately, then, a large number would be shot. From the percentage of marked rabbits in the kill the total population might be calculated. The relationships of the quantities may be expressed by the formula, $A/B = C/X$, in which X equals the total rabbit population and C equals the number of rabbits marked. A and B equal the marked rabbits shot and the total rabbits shot, respectively.

Accordingly on October 31 trapping was begun in the winter coverts (fig. 11, p. 371). During the following six weeks 92 rabbits were trapped and marked. In addition, eight rabbits were taken which had been marked during the preceding winter, and two which had been taken in a box trap set

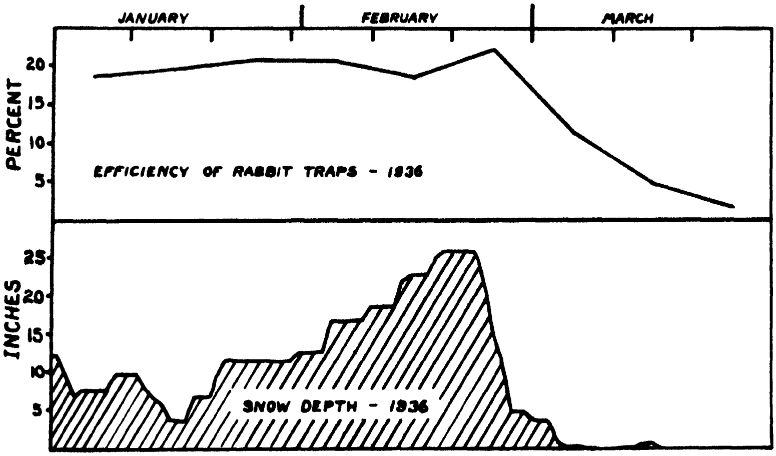

FIG. 12. Correlation of rabbit trap efficiency, as calculated by 10-day periods, with snow depth in January, February, and March, 1936.

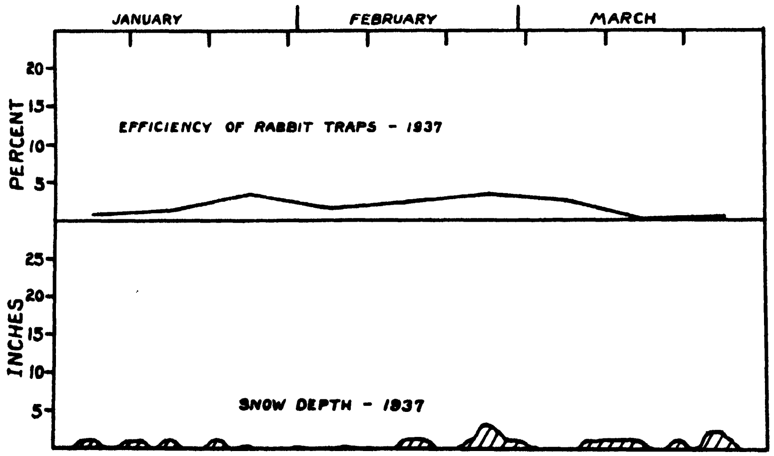

FIG. 13. Correlation of rabbit trap efficiency, as calculated by 10-day periods, with snow depth in January, February, and March, 1937.

for cats on the sanctuary a few weeks previously.[7] Thus a total of 102 marked rabbits were known to be alive during the period of six weeks and six days.

TABLE 3. RABBIT TRAPPING BY MONTHS; FALL AND WINTER, 1936-37

	November	December	January	February	March
New rabbits caught....	70	22	9	2	1
Total individuals handled (old and new) ...	73	61	21	19	7
Total repeats....	25	71	27	47	20
Trap nights	979	1,066	2,021	1,820	1,448

Individuals caught on Farm (in this period)..........114
Total rabbits marked to April 1........................181

[7] Several such traps were operated at various times and the few animals caught were turned over to me for marking.

On December 18, 19, and 20, in a systematic hunt covering the entire area, 126 rabbits were shot. As rabbits were killed the locations were marked on a map in the field (fig. 14). In the total kill 57 rabbits were found to be marked. The total population, then, was calculated as follows:

$$\frac{A}{B} = \frac{C}{X} \quad \frac{57}{126} = \frac{102}{X} \quad X = 225.4 \text{ rabbits}$$

Probably the most uncontrollable variable in a census of this type is the unrecorded mortality (and possible movement) that occurs among the marked animals during the trapping and shooting period. The shorter the period can be made the smaller will be this error. In the present census this figure amounts to what mortality occurred among a number of rabbits that progres-

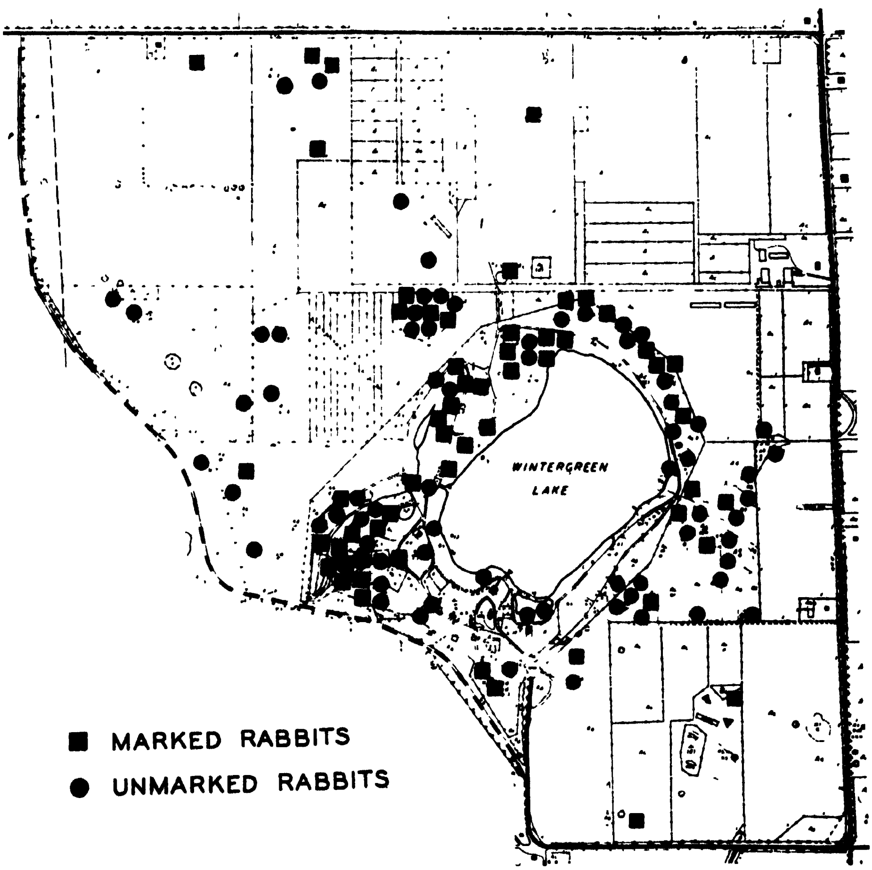

FIG. 14. Locations at which marked and unmarked rabbits were shot in the census of December 18, 19, and 20, 1936. Through an error in the field one unmarked rabbit is recorded here that could not be accounted for when the kill was examined.

sively increased from 1 to 102 in seven weeks. This is probably the greatest unknown in the census.

There are, however, other possible sources of error in this type of census. If any part of the farm had been intensively trapped and not intensively hunted, the indicated relationship of the members of the proportion would not be true. Also if any important rabbit habitat had not been trapped, but had been hunted, a similar error would be introduced. These possible inaccuracies were anticipated and every effort was made to include all of the rabbit habitats in both the trapping and shooting. It is believed that this was very efficiently carried out. On the map in fig. 14 are given the locations where every marked and unmarked rabbit was taken.[8] A comparison of this map with that giving trap locations (p. 371) will show that there was little disparity between the areas trapped and those shot over. If there was no great inequality one way or the other, it is quite probable that the minor errors of judgment would tend to cancel out. As for the mathematical errors of the count, these are dependent upon the size of the population and the percentages of the rabbits that were marked and shot. The population appears to have been about 226 animals; and of these 45 percent were marked, and 55 percent were shot. It is improbable that sufficiently large mathematical errors occurred to distort seriously the result.

Evaluation of Winter Inventories.—In considering the two census methods used it is evident that the one employed in the fall of 1936 is the most reliable. During the first winter of the work, trap efficiency was high (fig. 12). This is correlated directly with deep snow, which concentrated rabbits in cover patches and probably rendered the bait more attractive. Thus it was possible to handle a large part of the population, and what appears to be a good approximation of the number of animals present resulted. The census of the following fall showed the population to be much the same, but the winter that ensued was a season of little snow and comparatively high temperatures. Trap efficiency was low. Since, of the 226 rabbits indicated to be on the area, 126 had been killed in the census and 10 more had been shot in December hunting after the census, there were probably about 85 rabbits (allowing a few for animals shot but not retrieved in the hunting) on the area. Yet of this number only 27 individuals were handled in the next three months (as compared with 63 the winter before). Obviously the efficiency of the method first used depended upon weather conditions and would have been entirely inaccurate during the second season. The marking ratios method, however, was dependent upon traps only during seven weeks in November and December. During this period, despite a lack of snow, the bait in the traps was attractive to rabbits. The fact that the population was considerably more than 50 percent higher than it was late in the winter also probably contributed much to the efficiency of the traps and the success of

[8] These locations indicate, in all possible cases, where the rabbit was flushed. Where this was not definitely ascertained, the location at which the animal was first seen was used.

the method. From the results of this study the marking ratios method appears to be a reliable one for censusing rabbits on areas such as this.

In comparing the results of the two censuses for these two years a close approximation is obtained. In 1935-36 the census (calculated as of December 3) indicated 228 + rabbits. In 1936-37 an entirely different type of census (calculated for December 18) gave a result of 226 rabbits.

The fact that there was a difference of only two rabbits between the two counts does not, of course, indicate a proportionate accuracy in the censuses. Probably any one of the errors involved in either method is large enough to produce a greater discrepancy than this, even if the populations had been the same. The fact that the two census figures would fall within nearly any estimation of the values of the errors involved in each is the point of real significance. Since the second census was not subject to the most important unknown of the first (i.e. an unknown unhandled surplus of rabbits and the possibility of movement during the long trapping period) it may be considered, in a limited degree, a check on the first method. There is no guarantee that the populations were nearly the same, but there was no apparent difference in the numbers of rabbits present in the two years as judged by field observations during the hunting period.

As to the possibility of using other census methods, no other system proved feasible in this study. Attempted censuses with dogs proved to be hopelessly inadequate. Springer spaniels were used on bird censuses and the highest number of rabbits seen in a day of field work covering the entire area was 21. If enough men are used to drive cover patches, the possibility of counting individual rabbits several times is high. In addition, rabbits that are holed up will not be counted. Droppings and tracks have been useful indices of abundance in comparing habitats, but for estimating actual population numbers over a large territory, they have in the present case been found to be entirely unreliable. These results are in keeping with those of Trippensee (1934). He tried similar methods, which are described as (a) the sample area pellet count, (b) dog-census, (c) man count, and (d) track-feeding method. None of these was found to be satisfactory.

Spring Population, 1936.—The best clue to the size of the spring population on the Kellogg Farm comes from the trapping of February and March, 1936. An index may be obtained from the number of individual rabbits handled (and thus known to be alive) during this period of 60 days. Some rabbits doubtless escaped handling and some mortality (in rabbits counted) probably occurred. The difference between these two opposing errors is the real error.

In the trapping of February and March, 45 individual rabbits were handled (including both rabbits newly marked and old repeats). During most of February, trap efficiency was high, averaging near 20 percent. Rabbits were concentrated in cover patches where the box traps were located. When, how-

ever, the snow melted late in that month, rabbits apparently spread out and more green foods became available. Trap efficiency dropped to around 2 percent and continued low throughout March (fig. 12). Thus the chances of a rabbit's being handled after late February were considerably diminished, although during most of that month they were good. Considering these facts, and allowing a few for mortality, it seems likely that the April population of cottontails was near 50, or 25 pairs of potential breeders.

Productivity of Land.—If the above figures are used, a December (1935) population of near 228 cottontails furnished a hunting season kill of 154 and left a population which on April 1 was about 50. This spring breeding stock produced a December population of near 226. Of these, 136 animals were shot and approximately 85 were left, out of which another spring breeding stock would survive. In terms of land units the Kellogg Farm during these two seasons has in December supported one rabbit per 2.1 acres.[9] It appears to be possible for this area to produce consistently a hunting season crop of about 150 rabbits, or one rabbit per 3.2 acres of land.

Seton (1929) states, "It is established that no wild animal can stand a heavier drain than 20 per cent. per annum of its total numbers." Based upon this and using the estimated annual kill (100,000,000) he calculates the total population of the United States to be not less than 500,000,000 cottontail rabbits. Although the above conditions may hold for the country at large, it appears to be possible for a local population to support a considerably larger annual kill than that indicated. Unless the figures presented for the Kellogg Farm are subject to a much larger error than they appear to be, the population here has endured an annual toll of more than 50 percent. However, there may be conditions here, such as the large amount of coniferous cover, that render the area somewhat exceptional. This can be judged only when similar work is done on different territory.

Summary.—Box traps baited with an ear of corn were used in capturing rabbits. Under conditions of deep snow, trap efficiency was about 20 percent. Certain individual animals were inclined to develop trap habit. In one case a rabbit was taken 30 times in slightly more than two months. Rabbits were marked by tattooing a number in the right ear. By adding the total December kill to the total number of rabbits handled in the traps during January, February, and March, a minimum population figure of 228 rabbits was obtained for the winter of 1935-36. In December, 1937 a census by the "marking ratios" method indicated a population of 226 rabbits. The second census method was found to be the more reliable as it is not so much dependent upon weather and indicated a true population figure rather than a minimum one. The spring rabbit population (1936) of the Kellogg Farm was probably near 50. The December population density was apparently one rabbit per 2.1 acres. It is indicated that this area can consistently produce a hunting season crop of 150 rabbits, or one animal per 3.2 acres of land.

[9] On a basis of 480 acres of land (i.e. allowing for Wintergreen Lake).

Fox Squirrel

Oak openings in the primitive forest evidently were a most congenial habitat for the fox squirrel. It is not surprising to find the species common in this region where even yet, for an agricultural district, a comparatively large portion of the land is in oak woodland. The grazing of woodlots probably harms the fox squirrel less than any other game species.

Technique.—In the present investigation it was not possible to employ optimum trapping methods on every species dealt with. A much better study could have been made on the fox squirrel had this been the only consideration. These animals were taken in the box traps baited with ear corn. Although comparatively few traps were placed directly in oak woods, the extent to which squirrels travel on the ground rendered them comparatively efficient. The open wire trap is not well adapted to the handling of this species. These animals often fight furiously to break through the hardware cloth and sometimes succeed at the expense of torn claws, worn teeth, and a badly scratched head. Squirrels are very susceptible to shock and exposure to severe weather. As a result, many mortalities occur. In a total of 161 times that squirrels were handled in traps on the Kellogg Farm, 21 individuals were found dead.

During the first winter of the study these animals were marked by cutting a large V in the right ear. This did not designate individuals but merely indicated that the animals had been taken previously. During the second year individuals were marked by clipping a toe or a combination of two toes. Neither method is to be recommended. Ear notches in some marked squirrels appeared to heal over in a year until it was not possible to make sure the animals had been handled. Although there was no observed incapacity in toe-clipped animals, it would seem advisable to find a different method for an arboreal species.

Numbers Present in 1935-36.—During this winter fox squirrels were very abundant in the oak woods of the farm and sanctuary. In the winter trapping period 52 individuals were marked and 9 unmarked animals were recorded as mortalities. Thus 61 squirrels were handled, and this is an index figure for the early winter population. It is not certain that all of the squirrels were caught, nor is there any guarantee that all of those caught were resident within the limits of the Kellogg Farm. Tracks indicate that half a mile is no great distance for a squirrel to travel, and animals from Midland Park might well have been taken in the traps.

Numbers Present in 1936-37.—Due, evidently, to the action of a serious epizootic[10] in the spring and summer of 1936, the squirrel population in the fall of that year was considerably lower than in 1935. On the farm, squirrels

[10] A mange-like disease probably identical with that described by Errington (1933) appears to be endemic among the squirrels of this vicinity. In the spring of 1936 it appeared to spread widely among this species on the Kellogg Farm and in Midland Park. Numerous animals were seen with patches or nearly all of their hair missing, and several sick and dying squirrels were observed and others reported. An examination by Dr. Don R. Coburn, then pathologist of the Game Division, Department of Conservation, revealed no cause for the condition, which took the form of a severe dermatitis accompanied by extensive exfoliation of the skin.

were seen much less often, and in Midland Park the comparative scarcity of the species was even more manifest. The cottages in Midland Park are built among a uniform growth of oak trees. Protection from shooting has been practically complete, and squirrels have become very common. Any difference in numbers is readily noticed by residents here, and reports in the fall of 1936 were unanimous in the opinion that the number of squirrels had markedly decreased. Although from 20 to 40 box traps were operated from November 1 to December 18 on the Kellogg Farm, squirrels were caught only 8 times. However, this may have been partly due to the abundance of fall food (notably acorns) which made the corn in the traps less attractive. For the entire trapping period 24 individuals were marked and liberated and 15 unmarked squirrels were recorded as mortalities. The index population figure, then, is 39.

Evaluation of Data.—Considering everything, the figures 61 and 39 can be taken as fairly good indices of the numbers of animals present in the two seasons. The fact that more traps were used and more set in the woods during the second season would tend to neutralize any reduction in efficiency of operation resulting from the open winter. The fact that there were six weeks of trapping in the fall of the second season also tends to swell the total for that year. Any discrepancy in technique appears to be in favor of the 1937 period. However, the variables involved are too many and too little understood in the light of squirrel behavior to justify a more specific attempt to correct these figures.

Few population figures relating to squirrels have been found in the literature. One is cited by Seton (1929). Near Austin, Texas, in a "squirrel bush" of oaks, pecans, and red elms, an area of about 100 acres was alleged by a game warden to have a population of probably 500 fox squirrels. If this estimate and the figures given above for the present area are at all reliable, it would seem that even what appeared to be an abundance of squirrels at the Kellogg Farm in 1935 is not necessarily the maximum population density that the species may reach under some conditions. In the Texas area the population was about five squirrels per acre, while at the Kellogg Farm in the fall of 1935 the population was (on the basis of 61 squirrels and 30 acres of woodland) 2 squirrels per acre. As fluctuations appear to be an invariable characteristic of rodent populations under natural conditions, each of these figures can be taken to represent a temporary condition only. The true productivity of a habitat must be calculated by averaging the population numbers for a large number of years. For some sample areas in Missouri Bennitt and Nagel (1937) found that the maximum population density was one squirrel per 2 acres of woodland. They add that "—such a heavy concentration seldom occurs." For the southern half of that state they found that one squirrel per 8 acres was a fair average. Presumably these sample areas were open to hunting, and the numbers given may be applicable to similar conditions in

Michigan. Appearances seem to indicate that such a concentration as that of 1935 on the Kellogg Farm seldom occurs under ordinary conditions where the animals are hunted.

Eastern Skunk

Of the type of habitat favored by the skunk, Seton (1929) says, "—he loves variety—dry, rolling land, well watered, and alternated with sun and shade. In open fields, mixed with dense cover, he finds his ideal home." This might indeed be a description of the area around the Kellogg Farm, which certainly is very favorable to this species. Mr. William Parks, fur buyer in Augusta, reports that this area produced an excellent yield of skunk furs each season for many years before the establishment of the sanctuary. From 1927 to 1931 intensive predator control was practiced at the sanctuary and many skunks were killed. After that time smaller numbers were taken until the fall of 1935. During this investigation none was killed on the farm between the spring of 1935 and when animals were taken for breeding studies in 1937.

Technique.—Preliminary experiments during 1934 and 1935 showed that in fall and winter fresh carrion was an efficient bait for skunks. At the large poultry plant of the Kellogg Farm dead chickens were nearly always available. Hence the bait for box traps was standardized at one-half of a chicken. The box traps used were, in general, well adapted to the taking of skunks. Their chief disadvantage lay in the fact that skunks would, at times, tear a hole in the hardware cloth and escape. For skunks alone heavy-gauge, inch-mesh poultry wire would be preferable as a trap covering.

During the 20-month period from October, 1935 to June, 1937 a total of 143 individual skunks were handled on Section 8 or near-by. Of these, 83 were taken for the first time in box traps, 22 were dug from burrows, 31 were caught in steel traps, and 7 were found dead on the highway or elsewhere. Live skunks were handled 191 times and were taken in box traps a total of 165 times. The largest number of repeats for any individual was 6, and the average was 1.7.

Skunks were handled by covering the trap with burlap and dumping the animals into a bag. They were removed from the bag and manipulated by a hold on the base of the tail and the back of the neck. Marking as individuals was done by toe clipping and was satisfactory except for the tendency of skunks to lose toes in traps. There were a few cases of uncertain identity on this account.

Numbers Present in 1935-36.—The first skunk was captured on October 21, 1935. On January 2, 1936 the fourteenth skunk was taken. During the very cold winter weather no skunks were caught in the traps, and the next animal appeared on February 26. From then on skunks were taken regularly, and by April 12 a total of 30 different animals had been trapped and marked.

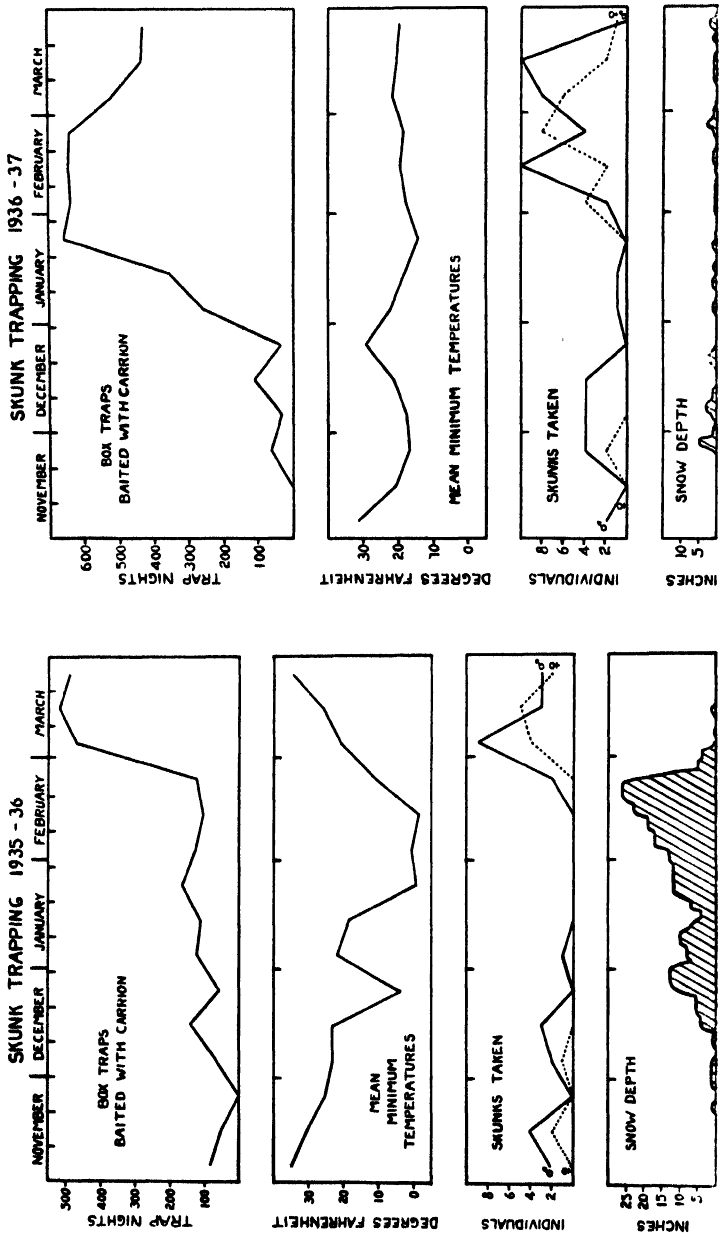

FIG. 15. Male and female skunks taken in box traps as correlated with temperature and snow depth in the winters of 1935-36 and 1936-37. Trap-nights, temperature, and skunks trapped are calculated for 10-day periods.

All of these were caught on the Kellogg Farm. Thus at least 30 different skunks were known to have been on the area during this period of 5½ months.

Upon examination of the sex ratio in this group of skunks, however, it was found that only ten were females. Subsequent work showed that a pre-

ponderance of males are handled in winter, due to a differential inclination between the sexes to remain holed up during cold weather. A similar condition was found by Cuyler (1924) in Texas and by Hamilton (1937a) in New York. In the 143 skunks handled in this study there were 79 males and 64 females, or a ratio of 0.447 females of the total population. It appears that there are fewer females because most of the animals were taken in winter when females were relatively inactive. Of 16 skunks handled from July to October (1936) 8 were males and 8 were females. In the light of these indications and subsequent results, it appears that the actual sex ratio here is 0.5.

Since 20 male skunks were captured over the winter, an equal number of females (presumably holed up much of the time) may, perhaps, be assumed; therefore a total of at least 40 skunks is indicated. This figure is not so well substantiated as would be desirable, but it is the best indication available of the number of animals which to a greater or lesser extent occupied the area during this period.

Numbers Present in 1936-37.—From September 17, 1936 until March 22, 1937 traps took 29 individual male skunks and 15 females on the Kellogg Farm (sex ratio, 0.34). During this season, however, 19 burrows (selected for appearances of occupation) were excavated, and these accounted for 2 males and 16 females that had not been handled previously in this trapping period. Thus the total catch was 31 males and 31 females (sex ratio, 0.5). Just what constitutes a "resident" skunk is difficult strictly to define, but as used here the word refers to animals that were using burrows on this area. Doubtless some of the skunks caught ranged in part over this area, although their customary burrows were elsewhere. This is supported by the fact that of 8 of the animals marked here 5 were retaken in the "turkey marsh,"[11] 2 in Midland Park, and one was followed to a burrow at nearby Duck Lake.

Since an intensive job of trapping was done during the early part of 1937, it appears probable that a large part of the male animals ranging over the farm were caught. The best indication of resident skunks, however, (not animals using the area, as was calculated for the previous season) comes from the females taken from burrows.

More than fifty burrows were watched during the winter, and it is fairly certain that those were excavated about which the most skunk signs occurred. As a number of females were in some cases concentrated in a single burrow (table 4) it appears that a few dens on the area contained most of the resident animals of this sex. In all, 22 females were accounted for by digging. Of the 15 females taken in the traps over the winter period, nine were not found in any of the burrows. Of these nine, however, one (skunk no. 1) had repeated five times (in 1½ years) and is almost certain to have been a resident. Of the other eight, three were later caught either in the turkey marsh or in Mid-

[11] A 60-acre area in an adjacent section of land to the northwest. It is owned by Mr. Kellogg, and the sanctuary turkey flock has been kept there—hence the name.

TABLE 4. RESULTS OF SKUNK DEN EXCAVATION; 1937

No.	Date (1937)	Locality	Situation	Skunks Found ♂	♀	Total	Remarks
1	1/12	Kellogg Farm..	Hillside in field.. ...	1	10	11	Burrow at least a year old
2	1/22	"	Bank of wash	0	0	0	Old burrow
3	1/22	"	Edge of wash .	1	0	1	Male from burrow no. 1, 1/12/37
4	1/18	"	Side of ditch bank .	1	10	11	Two skunks previously handled in traps
5	1/28	"	Open grassland ...	0	0	0	Old burrow
6	2/ 3	"	Sweet clover field	0	0	0	Old burrow
7	1/29	"	Under brush heap .	0	0	0	Old burrow
8	2/10	"	Island in swale.	0	0	0	Fresh tracks leading in and out
9	2/10	"	Grassy hillside . .	0	6	6	All from burrow no. 4
10	2/11	"	Sweet clover field	0	0	0	Tracks and fresh nesting material
11	2/12	"	Ditch bank	0	0	0	Tracks leading in and out
12	2/15	"	Lowland brush ..	1	0	1	Tracks leading in and out
13	2/12	"	Lowland brush .	0	0	0	Tracks plentiful
14	2/12	"	Lowland brush.	0	4	4	All from burrow no. 4
15	2/15	"	Base of tree .	2	0	2	A male opossum also in burrow. 1♂ skunk from burrow no. 4
16	2/16	Turkey Marsh	Upland woods . .	0	0	0	Old burrow
17	2/16	"	"	1	0	1	Male from burrows no. 4 and 15
18	2/17	Kellogg Farm	"	0	0	0	Very large nest of leaves; rabbit remains
19	2/18	"	Base of willow tree	0	0	0	Old burrow
20	2/18	"	Lowland brush	0	0	0	Old burrow; tracks
21	2/19	Duck Lake	Upland woods	0	0	0	Tracks numerous
22	2/19	"	Lowland brush .	0	0	0	Skunk had been followed into this burrow two days previously
23	2/25	"	"	1	7	8	None handled before
24	3/ 3	Kellogg Farm	Upland woods	0	1	1	Not previously handled
25	3/ 3	Turkey Marsh	"	1	1	2	Female skunk had been marked on K. F. 1/28/37 and retaken there 2/22/37
26	3/ 4	Augusta Creek	"	0	0	0	Skunk and opossum tracks

land Park and were probably non-residents. The remaining five skunks were taken only once, and there is a good chance that these also were non-residents.

Thus of a total of 62 skunks handled there were 23 females that good evidence indicates were residents (22 from burrows and 1 from traps). Since the work indicates an actual sex ratio of 0.5, one may probably assume an equal number of the males as residents. Thus on a basis of available evidence, the winter population of the 500 acres studied was about 46 skunks.

Evaluation of Data.—The work during the season of 1936-37 appears to be a much better population study than that of the winter before. In 1935-36 the severe weather rendered more skunks inactive, and as calculations were based on trap returns, the figures are probably low. Neither is it known what proportion of the calculated minimum of 40 skunks that used the area were actually resident skunks. It appears probable that, at least in this region, an intensive job of digging is the best method of censusing resident animals.

In terms of the winter census of 1936-37 the Kellogg Farm supported a resident population of one skunk per 10.4 acres of land. What the actual annual yield of fur would be, if the optimum number of animals were harvested, is not indicated. However, as the species is probably polygamous and as ordinary trapping in the winter when most females are holed up takes

many more males than females (Cuyler, 1924),[12] the annual fur crop probably does not inhibit the reproductive potentialities of the population so much as might be expected.

In the literature I have found relatively few estimates of population numbers for skunks. Seton (1909) states, "In the dry part of the pond and poplar belt of Manitoba, it would be safe to estimate the skunk at 1 to every square mile. In the prairie region, it is probably a fifth as numerous, and in the pine forest the number may be again divided by five." It is evident that the status of the Hudsonian skunk in Manitoba is much different from that of the Eastern skunk in Michigan. Of the latter species Norman A. Wood (1922) relates that at his home in Lodi Township, Washtenaw County, about 1870, more than 30 skunks were taken in one trap under an old barn. This sounds much more like the conditions found at the Kellogg Farm.

Bennitt and Nagel (1937) have calculated the skunk population of the state of Missouri for the winter season 1934-35. They considered the average litter to number six; thus the breeding potential of the females is 1:6. However, the most common number of young seen with an adult in the fall is four, giving an actual survival ratio of 1:4. The total kill by man for the year in question was 202,747. The mortality from natural causes was considered as one-third of the harvest by man. Hence the total mortality was near 270,000. On a basis of the above ratio of four young to one female, and considering the sex ratio in the "breeding reserve" to be 0.5, the spring population would be about 135,000 skunks. Since a decline in population was noticed, the authors believe that the actual size of this population was nearer 130,000 animals. These authors also drew attention to the fact that, in making such calculations, a pressing need is felt for more accurate information on the lives of animals. The values given to the necessary assumptions in such a census are no better than the facts at hand, and in our present state of enlightenment, a fairly large error is in some cases to be expected.

If the disproportionately large number of males taken in the trapping season in Texas as shown by Cuyler (1924), in New York as shown by Hamilton (1937a), and in Michigan as shown by the present work, holds good for Missouri, the sex ratio in the spring would not be 0.5, as assumed by Bennitt and Nagel. Hence if fewer males were present, and the animals are polygamous, the spring breeding population would be lower than that computed by these authors.

Ringneck Pheasant

According to local reports the region around the Kellogg Farm has never supported a large population of pheasants. In Michigan in general the pheasant appears to be most common on land that is more level and fertile than this farm. Pheasants have not been hunted on this area since it became a sanc-

[12] I am told by Mr. William Parks, fur buyer at Augusta, that not more than one-fifth of the skunks that he receives in late fall and winter are females.

tuary in 1927, and in the summer of 1933 the Department of Conservation liberated 150 birds as a test planting.

Technique.—Leopold (1931) has said, "It is more difficult to make a census of pheasants than of any other American species." From experiences here this view is entirely concurred in. The regular routine field work over the entire area gave a fairly consistent indication of the number of birds present. However, at intervals when men and dogs were available, the entire farm was covered in an effort to check all parts as simultaneously as possible.

During this study it was not found feasible to census pheasants before October on account of the height of herbaceous cover during summer and early fall. Even in October this difficulty was important, efficiency being higher in November and December. In this work an effort was made to traverse every part of the farm in one day. In several cases, however, a small portion had to be finished on the following morning. In these censuses men were lined up and spaced according to the density of the cover. Dogs were worked at intervals in front of the line of men. In open fields with snow on the ground the sphere of efficiency of a man and a dog was large. However, where even low cover was present a man was of little use, and the dependence was almost entirely on the dog (see also Wight, 1931). On several occasions it has been possible to stand quietly outside an area of brush and to see a pheasant double back and escape a dog without flushing. Even these animals do not put up every bird. A repetition of censuses was found to be necessary if accurate information on the number of pheasants present was to be obtained. There has been frequent interchange of birds with surrounding areas that very materially altered population numbers.

Daily field work on the farm has also revealed movements from or to the area and served to show population trends. In addition, box traps took pheasants fairly regularly, and the number of individuals trapped in the winter season was a significant index.

From the standpoint of a pheasant study the wire box traps used are not to be recommended. Birds in traps easily become frightened and almost invariably skin the top of the head while the traps are being approached. In this work pheasants have been taken in box traps 73 times and 7 mortalities have resulted from injuries so received. Wire funnel traps were experimented with but were found to be relatively inefficient as used here. A cat and a Cooper hawk caused the death of three birds in such traps. All but three mortalities due to technique were replaced by liberating birds of similar sex reared at the state game farm.

Pheasants were marked with leg bands and, during the second winter, tails were bobbed to a length of about 6 inches. This did not appear to impair the flying ability of the birds. Such bob-tailed pheasants were easily recognized in the field, although individuals were not indicated.

Population in Fall, 1935.—In 1935 the area was censused on October 14,

October 30, and December 20. The first two censuses were taken under conditions of high ground cover and only 400 acres were worked. Dogs could not at this time be used on the sanctuary. In the first census 29 pheasants were flushed, of which 14 were cocks and 15 were hens. In the second, which was relatively inefficient due to a lack of help, 20 pheasants were flushed of which 10 were cocks and 10 were hens. The census of December 20 was taken under more favorable conditions, the whole area was covered, and 28 pheasants were found. In the latter tally 14 were cocks, 13 were hens, and 1 was unknown. In this census it was felt that a fairly accurate approximation of the number of birds on the area was made. All indications point to an October population of between 30 and 35 pheasants on this 500 acres. Evidently the sex ratio was perfect. By December 20 the number was probably very close to the figure of 28 obtained in the census.

Field work showed that pheasants were well distributed over the farm during this period. At least four birds were known to be using the turkey marsh and the farm. In early fall hayfields and open areas were being much used, but by late December pheasants were most often found in thick brush or conifers. As an index to the late fall population the figure 30 may be taken as a reliable estimate. During the fall and winter 20 pheasants were taken in the box traps and banded. There were five recorded mortalities among unbanded birds. Hence, by this method 25 individuals were accounted for.

Population in Spring, 1936.—A census of the area on March 23 produced 20 pheasants, 6 of which were cocks, 13 were hens, and 1 was unknown. In April the localization of cocks on particular territories, as well as their crowing, made a check on the number of birds comparatively easy. It is fairly certain that there were about 12 hens on the area at this time and from 9 to 12 cocks. Of the latter only 4 or 5, as judged by their regular association with hens, appeared to be mated. During the winter 25 individual pheasants were handled. Five of these were mortalities, leaving 20 birds theoretically alive. Some of the latter may, of course, have left the area and others moved on. Only four broods are known to have been reared on this area and aggregated about 35 young pheasants in June.

Population in Fall, 1936.—A census on October 9, 1936 covering the farm (400 acres) but not the sanctuary showed a total of 22 birds flushed. Eight of these were hens, 13 were cocks, and one was questionable. At least a few pheasants were known to be on the sanctuary, which could not be worked with dogs due to the presence of migrant waterfowl. Evidently the fall population in 1936 was much the same as in 1935.

In December pheasants became fewer in number and by mid-January birds were seldom seen on this area. The pheasants from the farm had, for the most part, moved north and gathered in a large thicket of lowland brush southwest of Duck Lake. This covert lies just across the road from the northeast corner of the Kellogg Farm. Chicken house litter containing

cracked corn was being spread on the corner field of the farm and these pheasants at times fed here in a flock. The largest number counted was 24, but a flock of 15 to 18 was common. A census was taken on January 22 when this flock was absent. Only five pheasants (four cocks, one hen) were found. Few observations were made during the spring, but breeding birds were again back on the area.

Summary.—The number of pheasants present on the Kellogg Farm was indicated by censuses taken with men and bird dogs, by regular field work, and by birds taken in box traps. In late fall of 1935 the population was about 30 pheasants, with the sexes equal in number. The population density was about one pheasant to 16.6 acres. In the following spring the breeding population numbered about two dozen birds. In the fall of 1936 the population appeared to be much the same as in the year before. In winter, however, most of the birds of this area moved north into the next section, so that a census in January indicated only about five pheasants on the farm.

Quail

Quail populations in this portion of the state appear to be variable over small areas and short periods of time. The bird is not hunted as game in Michigan and hence its protection on the Kellogg Farm does not render the area exceptional in this respect.

Technique.—The quail population of this area was inventoried at the same time as were the pheasants; hence the same methods were used. As quail were in coveys during fall and winter, however, numbers could be fairly well checked merely by locating the coveys present. The principal difficulty was that during the winter quail were often in thick brush and had to be flushed to be counted. Accurate counts could, under these conditions, not always be made. In addition, the regular flushing of the birds disturbed them and evidently served to break up coveys. Catching a portion of a covey in a trap also tended to separate the birds. The interchange of quail between the different groups appeared to be frequent. In this connection Errington and Hamerstrom (1936) point out that they have made it a general policy not to do much banding or collecting on the areas where populations were to be observed under conditions as natural as possible. In some cases coveys could be checked by track counts without molesting the birds, but these occasions were relatively infrequent. In general, it may be said that work on this project appeared to disturb quail more than any other species that was studied.

Population in Fall, 1935.—In the first fall census (October 14) two coveys of 17 and 7 each were found. In the second of these five of the birds were seen to be juvenals. On October 30 three coveys were on the area and numbered 18, 17, and 5 quail respectively. One covey evidently moved onto the farm late in October. That daily field work was more reliable than infrequent inventories is shown by the results of the December census. At the

time of this inventory only 23 quail could be found. Yet during much of early December, field work showed that four coveys aggregating 42 birds were present. A bevy of 14 shifted onto and off the farm several times.

When snows became deep during January and February it was very difficult to follow the movements of the coveys. Birds shifted, ranges overlapped, and groups appeared to split and re-combine. It is doubtful whether by any method an accurate check could have been kept on these quail. A brief summary of observations will indicate the type of activity that occurred.

In January a covey of 14 that had been on the south side of the area (in December) disappeared as residents. They evidently moved south but reappeared from time to time, and 10 of the birds were trapped and banded. Half a mile south a woman began feeding from 15 to 20 quail and it is possible that some of these may have been all or a part of the covey of 14. On the north side of the farm a December covey of 15 also moved off the area, and soon after, 18 birds were seen north of the road feeding with a cock pheasant in a patch of corn. As three birds had also been flushed at times, it is possible that the 18 represented these plus the covey of 15. This is largely supposition, however, as the three may have moved south on the farm and joined other birds. A group of 10 quail near the middle of the area in December remained near a feeding station in January and were local in range but not always constant in numbers. Several times five or six birds flushed instead of the usual number. In February a covey of 15 quail appeared on the southwest side of the sanctuary and were fed there in a swale.

The nearest that I can come to tracing the history of a covey is one that was almost undisturbed in an experimental food patch in the turkey marsh. In February hemp projected above the snow and was fed upon by these quail, which roosted in the open. On February 11 there were 12 birds. Three days later there were still 12, but by the last of February the number had decreased to nine. On March 18 and 20 only six birds were flushed. Evidently the covey was breaking up at this time.

From the above discussion it is evident that any fixation of a population figure for this area in fall or winter would be somewhat arbitrary. The maximum population appears to have been 42, although shifts altered this considerably.

Population in Fall, 1936.—In late summer of 1936 it appeared that two broods that had been reared on the farm joined to form a covey of 25. In September these quail moved north into the turkey marsh and did not return to the farm area. During the fall and winter only 10 quail were present and these at times evidently moved into the next section to the north. The maximum population for the second fall season thus was 10. At times no birds at all were present, although there were bevies to the south and to the north on other areas.

There is little indication of the actual numbers on the area in spring. In

1935, 1936, and in 1937 quail were well distributed over the farm, and pairs were seen frequently. During the spring of 1936 as many as five calling males could sometimes be located almost simultaneously.

Summary.—The activity of quail has been characterized by frequent movements onto and off the area; thus populations have fluctuated radically. Evidently the maximum number of bobwhites that have been on the farm in two years is 42—the number present in early December, 1935. In late fall and winter of 1936-37 the maximum number of quail found was 10 and at times none at all was on the farm. On such a small area as this it is difficult to assign a numerical value to the quail population, due to the frequent changes resulting from the movements of coveys.

Species of Lesser Abundance

The New York weasel appears to be present in relatively small numbers throughout most of its range (Audubon and Bachman, 1849). Seton (1929) estimates its maximum numbers as a pair to the square mile during primitive times in Manitoba. From bounty records, he computes a population of about five to the square mile in Pennsylvania. The largest concentration of weasels that I have found recorded is indicated by Miner (1923), who took 57 of these animals in three traps during one summer. Tracks in winter were the best indication of weasel abundance on the area studied. On a basis of such evidence the weasel population of the Kellogg Farm was about half a dozen animals in January, 1937. Tracks were centered around such locations as a Microtus colony on the south side, the sanctuary woods, a buttonbush swale near the center of the farm, and the oak-hickory brush on the north side. Three weasels were taken in box traps during late winter. All of the animals handled were males.

The house cat has been one of the most consistent animals on the area from the standpoint of numbers and activity. In all kinds of weather cats have been found active, and whenever tracking conditions were good, field work indicated that from one to five animals had visited the area. During the first year of this work 30 individual cats were caught in the traps. Inasmuch as many of the animals taken were probably pets, they were kept for two days, in case they were called for. Of the 30 taken 23 were not claimed and were killed. During the second winter all that were caught were killed immediately and the stomachs preserved. Twelve cats were taken from September, 1936 to April, 1937. Evidently some of the animals found on the farm were abandoned by summer residents in Midland Park, and "drift" from other localities probably replenished the population here, much as on several areas cited by Leopold (1931). Only one case of breeding here is known, a female having borne a litter in one of the sanctuary buildings. The average number of cats on the farm at night was probably three or four.

The opossum has within the past 20 years extended its range northward into Michigan (Seton, 1929). At the Kellogg Farm it is not now abundant, opossums having been taken in traps only 30 times during the two winters of the work. Twelve individuals were marked by toe clipping. Three of these animals were juvenals taken in the fall of 1936. In the total of marked animals six were males and six were females. There is little to indicate the number of animals usually present, though from tracks and trap records in winter it probably was not more than three or four.

In summer raccoon tracks have frequently been observed in the swales on the sanctuary. Two of these animals were seen at dusk on an evening in October, 1934, and one (a female) was captured in a box trap in April, 1936. In accordance with the sanctuary policy it was necessary to deport the latter animal and liberate it elsewhere. There are several more sight records of raccoons and all were obtained in summer. No tracks have been seen after October, and the species was undoubtedly absent during the winter. Probably not more than two or three have been present at any one time in summer.

There is only one record of a red fox on the Kellogg Farm in two years. In January, 1937 tracks of one of these animals were present for several days and a fox was reported seen in the next section to the north. No other signs of the species have been found.

Woodchucks are not common on the area at present, although reports indicate that they were when the farm was established. Old burrows are very numerous, and doubtless many were originally dug by this species, although they are now used by skunks. Woodchucks have been seen only three times in three years. In addition, two specimens were caught in steel traps in the farm woods in the spring of 1937.

On one occasion (January, 1936) during the day two great horned owls were located almost simultaneously in the farm woods. Two birds have rarely been heard calling, but more than this are not known to have been present at one time. It may safely be said that ordinarily not more than one horned owl was on the area. Although regularly observed only in winter, the species was present intermittently in summer. In June, 1936 one of these owls was caught in a chicken coop a mile south. In June, 1937 young chickens were disappearing from the poultry yard on the Kellogg Farm. Steel traps were set and two horned owls were caught.

During the winter of 1935-36 from one to three Cooper hawks were regularly to be found on the farm. In the following winter the number was larger, appearing to vary from two to five. During the latter season three or four hawks could frequently be seen in the course of a day's field work. The difference in size between the sexes and in color between adults and juvenals often made it possible to count individuals with little chance for error. Most of the hawks seen on this area, however, have been juvenal females.

SMALL MAMMALS

Of the two species of ground squirrels on the area the thirteen-lined spermophile is by far the most abundant. Although their burrows are not found on cultivated ground, these rodents inhabit every grassy fence row and all the meadows and permanent hayfields, as well as the open areas on the sanctuary. No attempt has been made to compute the numbers of the species. It is sufficient to say that it is the most abundant mammal on the area larger than a mouse and that it is very commonly seen wherever there is open grassland.

The chipmunk is most plentiful in the farm woods, although nowhere does it reach the apparent population density of the foregoing species. In the spring of 1936 one pair inhabited the sanctuary woods. There appear to have been never more than two or three pairs on the entire sanctuary during this work. The species probably is not of great ecological importance on the area.

Flying squirrels were very infrequently seen during this study. Two were taken in steel traps in the turkey marsh and one was found dead in a box trap in the farm woods. Flying squirrels were observed in this woods on two occasions. Their strictly nocturnal habit makes observation difficult, although it is safe to say that they have been relatively uncommon on the area discussed.

Two species of mice are the most abundant mammals on the farm. In the fall and winter of 1935-36 both the prairie deer mouse and the meadow vole were very numerous. In long grass, thick alfalfa, or sweet clover, meadow mice were common, and many of their globular grass nests were found above ground. On the other hand, all of the open grass areas, hayfields, and even cultivated fields were occupied by the prairie deer mouse, so that for the area as a whole the latter species was very probably most plentiful. The dry summer of 1936 appeared to affect the field mice adversely. The population quite evidently was smaller in the following fall and winter than in the season previous. Many of the old colonies were entirely deserted. Numerous traps could be set in such places without taking an animal. A few colonies on the area, however, appeared to be as populous as ever. The drop in numbers seemed to be correlated with the drying up and comparative barrenness of localities that had supported a lush growth of grass or clover during 1935. There was no apparent diminution in the numbers of the prairie deer mouse, and in the second winter there is little question that the latter species was the most numerous mammal on the area.

The white-footed mouse was the most common small mammal in brush and woodland. The two species just discussed, with the addition of this mouse, form the bulk of the small mammal "key industry"[13] on the area. The woodland mouse, owing to its more restricted habitat, was not so abundant

[13] See page 400.

here as the prairie deer mouse or the meadow vole; although it was sufficiently numerous to be an important quantity in the food cycle.

The short-tailed shrew may, from its abundance, be added to the three species listed above as an important prey animal on this area. During the dry summer of 1936 it was common in the farm woods, though none could be taken in fields adjoining. In the following winter few were found in the woods, but the species was numerous in lowland brush. It was also taken in marsh grass on numerous occasions in winter. The very dry summer of 1936 apparently restricted this animal to low ground and woodland and may have reduced its numbers. Enough data are not at hand, however, to demonstrate this point.

The prairie mole was very plentiful during this study and probably of considerable ecological significance. Its tunnels were found on lawns, in pine plantings, and in grassland everywhere.

Only four individuals of the Cooper lemming-vole were trapped on the Kellogg Farm, and the species may be listed as very infrequent. Only two specimens of the pine mouse were taken, both of which were in the basement of the residence at the sanctuary. Jumping mice were caught on a few occasions in box traps, but less than a dozen individuals were caught or seen in three years. These three rodents are probably of little significance bionomically.

Masked shrews were not common on the area. Several were caught in mouse traps or found dead. Only one least shrew was taken. The star-nosed mole was not recorded during this study, but a specimen was captured on the sanctuary in 1933.

In summary, at the time of this investigation the most abundant small mammals, which form the small mammal key industry on the Kellogg Farm, were the thirteen-lined spermophile, prairie mole, prairie deer mouse, meadow mouse, white-footed mouse, and short-tailed shrew.

ANIMAL INTERRELATIONS

The purpose of the following discussion is to picture, insofar as possible with the data at hand, the mosaic of interrelationships that constitutes the life pattern of this area. Species are here considered chiefly from a qualitative standpoint, although little space is given to those that are not of sufficient size or present in sufficient numbers materially to affect the other animal populations. The more abundant upland mammals and birds, which characterize the area, are dealt with most completely in this section, as in the foregoing discussion of populations.

In treating the mutual effects of one animal species on another it appears most convenient to separate the subject into three major divisions. Animals are first considered from the standpoint of where they live. Species associated in the same habitats will obviously be most capable of close interaction. Time

of activity is taken as another point of emphasis. In the area studied the Cooper hawk is probably of little importance to the Virginia rail, as the former, although eminently raptorial in habit, is present only in winter; while the latter, definitely a prey species, is here only in summer. As another example, the screech owl probably seldom feeds upon the thirteen-lined spermophile, as the owl is nocturnal and the ground squirrel is exclusively diurnal. The third consideration has to do with the food habits of animals. This is, doubtless, the most vital relationship of all. It may be considered from two standpoints: animals of similar habit that compete for food; and the relations of carnivores to the species upon which they prey. Few species have been studied completely enough in this work to indicate many of the food relations occurring here. Hence the work of others is used wherever it is of significance. In general, what has been found true of a species on other areas can, if properly used, apply here. Such a method is considered definitely a part of this type of ecological research.

Habitat Relationships

If an attempt were made to describe transition zones and seasons, this discussion could well become unmanageable. Hence clearly defined types are chosen for analysis, with the understanding that a great variety of intergrading conditions exists. Habitats are arbitrarily grouped for discussion wherever on this area a similarity of use by animals appears to justify it.

Animals Associated in Summer Habitats

In most cases of common resident species certain habitat preferences have been manifest. The New York weasel is an exception to this. These animals or their signs were found in several types of habitat in summer, although observations were not numerous. Weasels in general have been observed in various situations (Burroughs, 1900; Nelson, 1918; Bailey, 1926; Leopold, 1937) and it is doubtful whether there is much of a summer habitat discrimination in this species. The animal is considered here to be a potential inhabitant of any of the following cover types and is not discussed under the separate headings.

Swales and Lowland Brush.—In the summers of 1935 and 1936 raccoon signs were common in the swales and around the margin of Wintergreen Lake. On one occasion two animals were seen together. Muskrats were always present in numbers during the summer season. These two species are the mammals most typical of this habitat, although in brush along swales the meadow jumping mouse was often found. The bird life was more varied. The great blue heron, little green heron, and the marsh hawk were regularly present, the least bittern, American bittern, and Florida gallinule occasional, the sora and Virginia rails frequent, and the mallard duck common. The most typical inhabitant of swales is the redwing blackbird. In and around the brushy margins yellow warblers, goldfinches, and song sparrows nested

commonly; and the catbird, brown thrasher, alder flycatcher, and kingbird were frequently seen. Pheasants (particularly cocks) were often found in lowland brush at this season.

Fields and Grassland.—The common summer mammals of this habitat are the skunk, house cat, cottontail rabbit, thirteen-lined spermophile, prairie mole, and prairie deer mouse. Woodchucks were present on the Kellogg Farm though not numerous. Where grass is deep the deer mouse is replaced by the meadow mouse. Both species have been found in alfalfa fields. The spermophile favors dry, open situations. On plowed ground skunks and the prairie deer mouse were the mammals most often found. The marsh hawk and crow were common over open grassland, and great blue herons not infrequently hunted here. Red-tail hawks often hovered low over the fields. Birds more properly belonging to the habitat in summer, however, are the ringneck pheasant, bobwhite quail, field sparrow, vesper sparrow, grasshopper sparrow, meadowlark, and horned lark. The bobolink, dickcissel, and Henslow sparrow occurred here sparingly at times.

Upland Brush.—In this habitat the skunk, house cat, cottontail rabbit, and white-footed mouse were common. In long grass the field mouse was nearly always present. Some woodchuck dens were also found in upland brush. The birds ordinarily found here were the catbird, brown thrasher, cardinal, goldfinch, mourning dove, chipping sparrow, pheasant, and quail.

The upland coniferous plantings have a well-defined fauna apart from the deciduous type. The cottontail rabbit, the common mole, and the white-footed mouse were nearly always present; and in thick grass the meadow mouse was common. Robins and mourning doves nested abundantly in the conifers, and catbird nests were not infrequent. Pheasants, paricularly cocks, were often seen here in summer. The small spruces and junipers were especially favored by the chipping sparrow, which nested regularly in this type of cover.

Woods.—The summer population of the upland woods is typified by the fox squirrel, flying squirrel, chipmunk, white-footed mouse, and short-tailed shrew. The latter species showed an especial preference for this habitat during the very dry season of 1936. Woodchuck dens were common here, but skunks appeared to be only occasional in summer. Rabbits also were relatively infrequent. The avifauna is characterized by the crow, red-tailed hawk, red-headed woodpecker, flicker, great crested flycatcher, wood pewee, red-eyed vireo, warbling vireo, Baltimore oriole, and blue jay. So little lowland wood being present, it is not characterized by a well-defined fauna on this area. It has been noted, however, that several opossum dens were in this type of habitat.

Animals Associated in Winter Habitats

Fields and Grasslands.—One of the most typical inhabitants of this type of territory is the prairie deer mouse. In situations having a dense growth

of Kentucky bluegrass, alfalfa, or sweet clover, winter colonies of the meadow mouse have often been present. Under deep snow, however, Microtus colonies have been observed to move into upland brush or coniferous plantations where they were not present in summer nor in winter when snow was absent. Weasels were frequently found around mouse colonies, short-tailed shrews have been taken in the runways, and skunks were at times active here during periods of mild weather. The prairie mole is most typically found in grassland. House cats hunted this habitat under all conditions. In the winter of deep snow (1935-36) flocks of from 10 to 100 tree sparrows and juncos, with a few song sparrows, were common in the open fields. Horned larks, in flocks of a dozen or so, were also present. In February, when the snow reached a depth of one and one-half feet the flocks began to disappear until, late in that month, few of these birds were to be found on the area. In the mild winter of 1936-37 there was little snow until March. The songbird flocks of the preceding winter were conspicuously absent. At times hardly half a dozen tree sparrows and juncos were to be found, and horned larks did not arrive until mid-February. Quail and pheasants have been found in the open under many conditions, though most often when snow was not deep. When snow was absent, pheasants regularly fed in the fields. Crows were active in this habitat regardless of conditions.

Swales.—When swales were frozen, the marsh type of cover was used by cottontail rabbits, meadow mice, prairie deer mice, short-tailed shrews, and masked shrews. The most typical mammalian inhabitant is, of course, the muskrat. The marsh grass and cat-tail have also served as cover for pheasants and quail upon occasion. Nearly all of the songbird species listed for grassland have used the marsh in much the same manner.

Brush.—In winter lowland brush functions much the same as upland brush for most species. The muskrat, however, is more common in and around the lowland brush areas, and the short-tailed shrew has been found in greatest numbers in such situations. Both upland and lowland types are extensively used by the cottontail, weasel, skunk, house cat, and white-footed mouse. Pheasants and quail are very dependent upon brush cover in winter, and the Cooper hawk was most often found in such areas. Among smaller birds the cardinal, blue jay, chickadee, downy woodpecker, song sparrow, junco, and tree sparrow were common. Conifers were most favored by rabbits and pheasants as winter cover. The Cooper lemming mouse was taken several times in conifers and also in upland brush.

Woods.—The fox squirrel is most typical of this habitat in winter. Skunks, house cats, weasels, rabbits, and white-footed mice are the other mammals that have been found here. Among birds the crow, great horned owl, and Cooper hawk were winter inhabitants, as were the white-breasted nuthatch, chickadee, and downy woodpecker.

Use of Dens

Old woodchuck dens were numerous, although only a few woodchucks were to be found on the Kellogg Farm during this study. Skunks use practically any kind of burrow, including woodchuck dens, as well as those dug by themselves (Nelson, 1918; Seton, 1929; Johnson, 1930; Goodwin, 1935). Such holes undoubtedly form important winter cover for rabbits (Trippensee, 1934; Tubbs, 1936). Rabbit tracks have frequently been seen leading into burrows which skunks were known to have used at some previous time. When water was low in winter they also occupied old muskrat burrows. Weasel tracks and tracks of the white-footed mouse have been found which indicated a use of such dens. One skunk den that was excavated contained two skunks and an opossum.

Dens may be considered to affect the interrelations of animals in two principal ways. The construction of burrows by the woodchuck and the skunk may abet the efforts of a rabbit to escape from enemies above ground and contribute to its comfort during severe weather (Leopold, 1931; Trippensee, 1934). These same burrows, however, may serve the weasel and skunk in enabling them more easily to catch the rabbit (Audubon and Bachman, 1849; Kennicott, 1858; Stone and Cram, 1920). The weasel in particular uses its small size and sinuous body to good advantage in entering the burrows of small animals. Bailey (1926) states that on the plains it regularly enters the burrows of pocket gophers. Audubon and Bachman (1849) and Seton (1929) refer to its pursuit of mice and ground squirrels into their homes. Kennicott (1857) and Cory (1912) speak of weasel nests in "deserted" ground squirrel burrows. During this study weasel tracks were very frequent around winter colonies of Microtus. In the tunnels under deep snow these animals were probably protected from most other enemies. A weasel has been seen dodging in and out of the burrow of a mouse, and its stomach was found to contain the remains of the burrow's probable owner (*Peromyscus* sp.). A vivid impression remains that this animal is primarily adapted to hunting in small holes. Such burrows, coupled with the weasel's capacity for over-indulgence in the matter of killing (De Kay, 1842; Coues, 1877; Merriam, 1886; Lantz, 1923), appear to make it possible for a small number of weasels to be a material factor in the lives of a very large number of Microtines and other Rodentia.

Activity Relationships

As elsewhere pointed out, animals are brought into most direct contact with one another, first, by being in the same habitat; and secondly, by being active at the same time. This is not, by any means, the only way that species interact; but it is the principal way in which predator-prey food relationships are brought about. As a consequence, it is considered important in this discussion.

Seasonal Activity

Certain species which are undeniably important as bionomic factors on this area are of seasonal occurrence only. An animal may be designated a seasonal either because it is present and dormant, or absent through migration. Predominants are present and active through the year.

Predominant Animals.—The carnivorous mammals which are regularly present and perennially active on this area are the house cat, weasel, opossum,[14] prairie mole, short-tailed shrew, and masked shrew. The winter activity of the mole has been questioned, but the animal is now known to be active throughout the year (Scheffer, 1927; Gregory, 1936). Fresh workings during the winter have often been seen in the course of this study, and on January 10, 1936 a specimen was found above ground burrowing about through an inch of snow.

Among the herbivores the cottontail, fox squirrel, muskrat, prairie deer mouse, white-footed mouse, Cooper lemming-vole, and meadow mouse are predominants. In this work no flying squirrel records have been obtained in winter. The consensus of opinion, however, is that the animal does not hibernate (Kennicott, 1856; Anthony, 1928; Gregory, 1936), although it is believed to be inactive and to remain in the nest during very cold weather (Merriam, 1886; Wood, 1910; Nelson, 1918; Stoner, 1918; Stone and Cram, 1920). In this case it may be listed as predominant.

Predominant birds on this area are the pheasant, quail, screech owl, crow, mourning dove, flicker, hairy woodpecker, downy woodpecker, blue jay, chickadee, starling, English sparrow, goldfinch, and song sparrow. The great horned owl is a regular winter inhabitant but is, apparently, only occasional here in summer; hence it is not included in the above. The goldfinch and song sparrow have been present in winter in small numbers only. The horned lark was present throughout the winter of 1935-36 but did not arrive until February in 1937. It is ordinarily not predominant, but a late winter and summer resident.

Seasonal Animals.—The annual migration of most birds and the winter dormancy of certain mammals give the winter and summer vertebrate populations of the Kellogg Farm materially different aspects.

Species that are dormant in the winter are the woodchuck, spermophile, chipmunk, jumping mouse, and the skunk. Skunks do not hibernate, as do the other species, but remain inactive in dens during the coldest part of the winter. A thaw will find some old males abroad, but during January and February the number of active skunks is small.

Of the migratory birds that visit the area a few species are present only in winter. Such residents that leave in spring are the Cooper hawk, great horned owl (with exceptions), tree sparrow, and junco. Snow buntings, redpolls, and siskins are only occasional.

[14] Opossums have, however, been inactive during very cold weather.

With regard to summer populations, all of the mammals listed as predominant or dormant in winter are, of course, active in summer. One species, the raccoon, has been found on the area only in summer. At this season a few individuals intermittently fed in the swales. No raccoon signs were found in winter or spring. Evidently these animals had their dens on some near-by area.

Most bird migrants are found in this locality only in summer. The following species were regularly present during three seasons: pied-billed grebe, great blue heron, little green heron, black-crowned night heron, American bittern, least bittern, Canada goose, mallard duck, red-tailed hawk, marsh hawk, Virginia rail, sora rail, coot, killdeer, spotted sandpiper, herring gull, ring-billed gull, black tern, black-billed cuckoo, nighthawk, chimney swift, hummingbird, kingfisher, red-headed woodpecker, kingbird, great crested flycatcher, phoebe, alder flycatcher, least flycatcher, wood pewee, prairie horned lark, tree swallow, bank swallow, rough-winged swallow, barn swallow, purple martin, house wren, catbird, brown thrasher, robin, bluebird, starling, red-eyed vireo, warbling vireo, yellow warbler, meadowlark, redwing, Baltimore oriole, bronzed grackle, cowbird, towhee, grasshopper sparrow, vesper sparrow, chipping sparrow, and field sparrow.

Species in the check-list (see appendix) that are not discussed here as to seasonal activity either have occurred sporadically or have been recorded only during the spring and fall migration seasons.

Daily Activity

Among the predominant animals of the Kellogg Farm the following are chiefly nocturnal: house cat, opossum, rabbit, muskrat, prairie deer mouse, white footed mouse, and flying squirrel. The last three named appear to be exclusively nocturnal. All the others have been seen abroad in the daytime. From records secured in this work weasels appear to be active at any time through the day or night. This is in agreement with the findings of Coues (1877), Herrick (1892), and Nelson (1918). Kennicott (1857) considered weasels to be principally nocturnal. As for the short-tailed shrew, few records of daytime activity have been obtained here, but Nelson considers it to be active with little regard to the time of day, and Williams (1936) found it active both day and night. All other of the perennially active mammals are diurnal.[15] Of the birds listed as predominant the screech owl is the only nocturnal species. All others are diurnal.

Of the species present in summer the skunk is for the most part nocturnal, though individuals have been seen at various hours throughout the day. Raccoons are doubtless nocturnal, although one morning observation was made. The jumping mouse has been seen several times in the daytime, although the species is nocturnal (Kennicott, 1856; Seton, 1909; Nelson, 1918). The

[15] Few data have been obtained here regarding the activity of meadow mice, but Hamilton (1937b) found them to be chiefly diurnal with activity greatest in early morning and late afternoon.

woodchuck, spermophile, and chipmunk are diurnal. Other mammals active in summer have already been discussed. Of the summer birds the screech owl has been cited as nocturnal. The night heron is crepuscular and nocturnal. The great blue heron is active both day and night, as is the nighthawk. Intensive study has not been made of the marsh and shore birds, though most are active by day and, except during migration, appear to be relatively inactive at night. Nearly all the smaller birds are diurnal.

Most of the winter birds and mammals have been referred to under predominants. Of the seasonal species the great horned owl is nocturnal and the tree sparrow and junco diurnal.

Food Relationships

Plant and animal populations are most effectively unified into ecological communities through the absolute necessity of each individual in every species for food. Considering the patently fundamental place of plants and invertebrates in the food relationships of animal society, a discussion of birds and mammals alone necessitates a somewhat artificial simplification. No attempt is made here to treat even the latter groups completely. Certain phases of the subject have been investigated which appeared to be important to the status of one or several of the more influential species, and which seemed to be amenable to logical analysis under the existing conditions.

Elton (1927) resolves the food relations of animals into four principles which he designates as follows: (1) food chains and the food cycle, (2) size of food, (3) niches, and (4) the pyramid of numbers. It will be profitable to review the implications of each of these principles.

Herbivores are the fundamental class in animal society, and through them the energy derived by plants from sunlight is transferred to all the carnivores. Food habits among carnivores differ widely, certain species being preyed upon by certain other species, which may in turn be eaten by still larger forms. Thus chains of animals are formed, linked together by food. These may extend from the smallest herbivores up to the largest carnivores which dominate the community. The aggregate of all the food chains in a community is spoken of as a food cycle. As each species in a food chain is usually larger than the species below it, the principle of size of food is introduced. Animals utilize food within certain size limits because species above these limits are too large to be killed and species below are too small for the numbers that can be eaten. Thus an animal occupies a specific place in a community because it utilizes food of a certain size. The plan of communities everywhere is much the same, and although species of similar habit in widely separated communities may differ in taxonomic position, their functions or "niches" in the ecological structure may be essentially the same. One well-defined niche is that of herbivorous animals that are so numerous as to support a large number of carnivores. These herbivores form what is termed a "key industry," a

good illustration of which would be the small mammal key industry that occurs nearly everywhere. It will be observed that, progressing downward in the food chain, one finds that as animals decrease in size they increase in numbers; so that, considered numerically, food relationships can be represented by a pyramid with a multitude of small animals at the base, smaller numbers of animals intermediate in size in the middle, and finally tapering off to a few individuals of large species at the top. Enough data are not available to treat the fauna of the Kellogg Farm completely from all of the angles cited above. These conceptions stated by Elton are considered, however, a fundamental preface to any discussion of food relations, as they create a pictorial structure in which can be placed any apparently disconnected facts which are brought to light.

Food Relations of Herbivores

Inasmuch as herbivorous species do not habitually utilize one another as food, their most apparent food linkage is through competition for a common supply. In summer this rivalry has not appeared to be intense, as the superabundant vegetation present on this area has evidently been more than enough to supply the needs of all. In winter the problem is vital, as food supplies may be used up or become less available through deep snow. The present study treats the winter season only.

Herbage Feeders.—Two species of mammals, rabbit and meadow mouse, are the most influential herbage feeders on this area. The muskrat belongs more properly to the aquatic habitats and was not intensively studied. Animals that feed upon the leaves and stems of plants may not only compete for food but, through the girdling of shrubs and trees, destroy cover that can materially affect future winter populations of both carnivores and herbivores.

Rabbits eat a great variety of herbaceous vegetation (Seton, 1909) and apparently prefer this type of food. In the very open winter of 1936-37 very little bark of any kind was taken. A winter staple on the Kellogg Farm is buckhorn. Under conditions of less than an inch of snow rabbits often scratched through and fed upon this plant.[16] Yarrow is another herb that was so taken, and rabbits have been seen eating dandelion and bluegrass.

Under the conditions of very deep snow existing in the winter of 1935-36 very little herbaceous vegetation was available and, apparently as a consequence, rabbits fed extensively upon bark. These rodents use woody plants as food by pruning, budding, and gnawing the bark from the stems. Kennicott (1857) found that pruning was the type of work most frequently found in orchards. However, on the Kellogg Farm bark feeding was of more frequent occurrence than pruning. Feeding upon woody plants by rabbits has been described by Audubon and Bachman (1849), Lantz (1907a, 1929), Todd (1927), Nelson (1918), Stoner (1918), Trippensee (1934), and Siegler (1937).

[16] Kennicott (1857) states that rabbits seldom, if ever, dig through the snow, and this has usually been found true where its depth was an inch or more.

FIG. 16. Staghorn sumacs barked by rabbits during the winter of 1935-36.

On the area treated here dwarf sumac and staghorn sumac were the two species that were most often taken. Figure 16 shows the "rabbit line" on staghorn sumacs in a kettle hole near the farm. Twenty-eight species of woody plants were observed to be used, among which were willow, sassafras, wild crab apple, buckthorn *(Rhamnus cathartica)*, wild black cherry, elder, rose, grape, and several species of dogwood. Oak and even hickory were eaten in some places. Although the work of rabbits was widespread and easily noticed in winter, it was of little actual significance in reducing cover on the area.

Meadow mice are known to live to a great exent upon grass and other green herbaceous food; but in winter, especially when snow is deep, they eat the bark from nursery stock, shrubs, and trees of many kinds (Kennicott, 1856; Butler, 1892; Herrick, 1892; Bailey, 1900, 1924; Lantz, 1907b; Evermann and Clark, 1911; Cory, 1912; Nelson, 1918). On the Kellogg Farm in the winter of 1935-36 meadow mice extended their range under cover of the deep snow into tree and shrub plantations where they had not been numerous before. After the snow melted, twelve species of trees and shrubs were found to have been girdled by these mice. The most extensive girdling was done on Scotch pine. In the turkey marsh to the northwest of the farm, in a planting of 97 pines only 27 trees escaped damage and about 50 were killed (fig. 17). Other conifers that were taken were western yellow pine, Austrian pine, and ground juniper. In a mixed planting of white, western yellow, and Austrian pines on the farm nearly all of the latter two species were girdled, although white pines were found to be untouched. Deciduous shrubs and

FIG. 17. Scotch pines girdled by meadow mice in the winter of 1935-36. The tree in the right foreground is about 5 inches in diameter.

trees that were preferred by the mice were mulberry *(Morus rubra* and *M. alba),* wafer ash or hoptree (*Ptelea trifoliata*, fig. 18), wild black cherry, honeysuckle (several cultivated species), and catalpa (*Catalpa speciosa*, fig. 19). In a near-by orchard apple trees had the lower limbs barked where they were covered by snow. In the winter of 1936-37 very little bark was taken by mice. This is probably due in part to the fact that field mice were fewer in numbers, but may be ascribed principally to the lack of snow. As a result herbaceous plants were available, and there was no protection for the aboveground activities of the species.

The work of rabbits and meadow mice is not difficult to distinguish. Rabbits leave ragged edges and do not take the bark cleanly, whereas the mice remove it smoothly down to the white wood and completely lay bare the area worked upon. Rabbits eat bark above the level of the snow; and all of the observed mouse girdling has been done in tunnels beneath its surface.

Woody vegetation has been sufficiently abundant on the area studied to obviate the necessity for any intense competition between the rabbit and meadow mouse for this type of food. Meadow mice have done more to reduce

FIG. 18. Wafer ash or hoptree (about 1 inch in diameter) girdled by meadow mice during a period of deep snow.

cover, due to the species attacked, than rabbits; however, all of such rodent activity together has not been sufficiently intensive to affect materially the amount of cover present. Hence, notwithstanding the potentialities with which the above habits are fraught, they are probably not of great significance to other species on this area.

Seed and Fruit Feeders.—During most growing seasons plants of every description produce large quantities of fruits and seeds. These ripen in the fall and form a progressively diminishing food supply during the winter for certain ground-feeding birds and other animals. In the fall of 1935 on this 500 acres a collection of more than 90 species of such fruits and seeds was made. Only those were taken which appeared to be usable by winter birds as food or were listed by some author as such. Some fruits disappeared during the fall. Of those that were more persistent a record was kept of the length of time during the winter that they remained apparently available as a food supply for birds. Table 5 in the appendix gives the approximate abundance and duration of availability of 81 species. This represents the winter season of 1935-36 only and can not be taken as indicating the ordinary relative per-

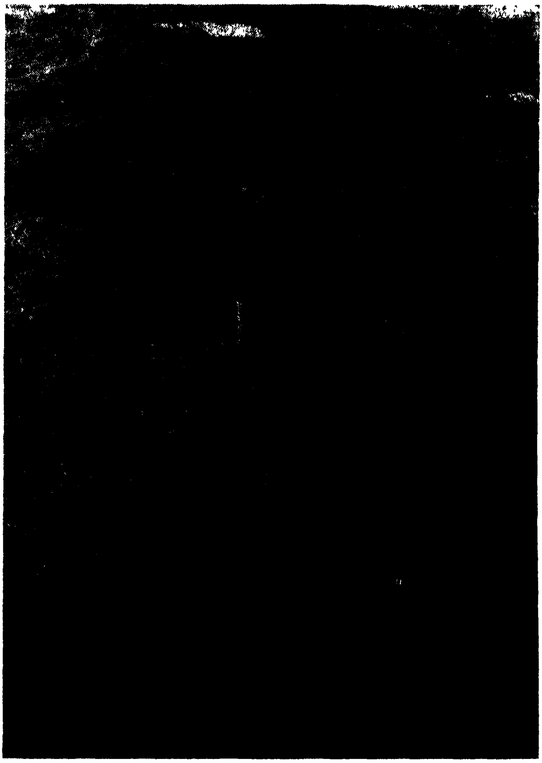

FIG. 19. A 3-inch catalpa tree girdled by meadow mice. The upper limit of the bare area represents the snow level.

sistence of the various species. Some were buried under two feet of snow and others were almost entirely used up by the birds feeding upon them. In general, fleshy fruits disappeared early, leaving the dry fruits of grasses *(Poaceae)*, buckwheats *(Polygonaceae)*, and other common weeds found on cultivated ground as the most important winter foods of seed-eating birds and mammals. Cultivated grains were present in certain feeding stations and rye patches, but did not greatly interfere with the study of natural foods.

On the Kellogg Farm from point of size, the ringneck pheasant is the largest animal dependent upon grain and seeds in winter. That the species utilizes quantities of the common weed seeds as food has been shown by many investigators (Leffingwell, 1928; Forbush, 1929; Swenk, 1930; Beebe, 1931; Green and Beed, 1936; Dalke, 1937; Gigstead, 1937). A total of 70 fall and winter stomachs were obtained from hunters and by other means in this and near-by counties. A qualitative examination showed ragweed, green and yellow foxtail, several species of smartweed and bindweed, and other common weeds to be frequently taken. Corn and other cultivated grains were

present in quantities. The crop of a hen shot on February 3 contained rye, vetch, and dodder. Burdock, bittersweet, and grape were also often eaten in late winter.

The bobwhite quail utilizes similar foods in winter (Judd, 1905; Nice, 1910; Errington, 1930, 1931; Bird and Bird, 1931; Handley, 1931; Leopold, 1931). Eleven fall stomachs from this vicinity yielded quantities of ragweed, foxtail, panic grass, and buckwheat. Bobwhites are known to be particularly fond of legumes, and two of these stomachs contained the seeds of sweet clover (*Melilothus* sp.).

In the winter of 1935-36 a large portion of the natural food supply of the area was taken by flocks of songbirds. Tree sparrows and juncos were particularly abundant, and horned larks were common. The food habits of these birds have been studied by Judd (1898), McAtee (1905), Beal and McAtee (1912), and Gabrielson (1924). It has been fully demonstrated that common weed seeds form the bulk of their winter foods. A collection from this area of 124 stomachs (principally of juncos and tree sparrows) was made in December, January, and February. A qualitative analysis showed that 30 species of fruits and seeds had been taken as food. Following is a list of the 10 species most frequently taken and the number of stomachs in which traces or quantities of the food were found:

Ambrosia elatior (ragweed)	73
Chenopodium album (lamb's quarters)	54
Poa spp. (bluegrass)	27
Nepeta cataria (catnip)	23
Amaranthus retroflexus (redroot)	21
Monarda fistulosa (wild bergamot)	14
Rumex acetosella (sheep sorrel)	9
Amaranthus graecizans (tumbling pigweed)	8
Sporobolus spp. (dropseed grass)	8
Setaria lutescens (yellow foxtail)	7

Two other species of animals are of undoubted importance as feeders upon weed seeds. Although all mice appear to use this food to some extent, the white-footed mouse and prairie deer mouse are notable for the habit (Audubon and Bachman, 1849; Kennicott, 1856; Merriam, 1886; Seton, 1909; Cory, 1912; Nelson, 1918; Stoner, 1918; Bailey, 1926; Johnson, 1930; Gregory, 1936). As has been pointed out by Dice (1922) and Johnson (1926), a well-developed habitat selectivity is shown by these two species. The prairie deer mouse inhabits the open fields, and the white-footed mouse is a woodland form. On the Kellogg Farm one of the two is found everywhere except in very wet marsh. The prairie species is widely distributed in the open fields and grassland, while the woodland mouse inhabits all of the woods and brushland. The only habitat where both have been found is a grassy area sparsely planted to small conifers.

As a consequence of this habitat preference the food of *P. leucopus nove-*

boracensis contains a higher percentage of nuts and tree seeds than that of *P. maniculatus bairdii.* Osgood (1909) states that the former is very fond of basswood seeds, wild cherry pits, and acorns. Both species lay up winter stores, but both are also active foragers in all kinds of weather. From the standpoint of weed seeds all evidence points to the prairie deer mouse as the most important competitor of ground-feeding birds. A nest of this species that was excavated in January, 1937 contained approximately a pint of seeds of bush clover (*Lespedeza* sp.), ragweed, wheat, black bindweed (*Polygonum convolvulus*), yellow foxtail, campion (*Silene* sp.), and field sorrel. Tracks in the snow showed that this mouse regularly fed upon ragweed, tumbling pigweed, and lamb's quarters.

Two winters' observation on this area indicates that the intensity of competition for the above type of food depends principally upon the depth of winter snow. Deep snows quickly reduce the supply of available foods and concentrate the efforts of all species upon what remains. The nature of the growing season or other factors may determine the amounts of some foods that are produced. The drouth in 1936 evidently curtailed the crop of arrow-leaved tear-thumb and certain other species. However, the harvest from common weeds such as ragweed, lamb's quarters, amaranths, and others appears to be a very dependable quantity. These types made an excellent growth during the hottest part of the summer in 1936, when the ground was very dry and dusty four feet beneath the surface.

The very deep snow in the winter of 1935-36 rendered unavailable the low-growing foods such as field sorrel. Hence the dependence of nearly all seed-eating animals was upon ragweed, lamb's quarters, redroot (fig. 20), bergamot (fig. 21), and such other species as projected above the snow. Ragweed was the most abundant of these, and by the middle of February plants of this species had been almost completely stripped of their fruits. When such a condition was reached, the flocks of songbirds almost entirely left the area. Where before several hundred tree sparrows and juncos had not been unusual, hardly a bird was to be found. Errington (1930) refers to a season of deep snow when the ragweed supply was exhausted by the middle of January. In speaking of quail the same author (1931) calls attention to the "—terrific food competition furnished by small birds, ringnecked pheasants (in one area) and rodents—."

Considering the widespread and intensive activity of mice and songbirds, it appears that these animals took the greater part of the winter's supply of seeds. The fact that the mice stored food in quantities, and the ability of the songbirds to abandon the area if necessary leaves the pheasant and quail as the species most likely to suffer in case of food shortage. The shortage in February, 1936 did not last, as the deep snows melted late in that month. Pheasants found enough burdock, dodder, vetch, grape, bittersweet, and cultivated grains to satisfy their needs. Quail used such foods as sumac drupes

FIG. 20. Redroot upon which snow buntings fed above two feet of snow in February, 1936.

and ash samaras, or moved about until a feeding station, shocked corn (on near-by farms), or other supply was found. No starvation or decline in health was observed among the birds on the Kellogg Farm.

Evidently this is another relationship which, under some conditions, might seriously impinge upon two resident species, the pheasant and the quail. Under the conditions studied, however, the food shortage induced, in part, by mice and songbirds did not result in a loss of life among the game birds. In the following winter (1936-37) the supply of food available was much larger than in 1935-36, due to the small amount of snow on the ground. In that season very few songbirds were present; most of the pheasants and quail moved to adjoining sections of land; and the mice, evidently, were left in control of a food supply much in excess of their needs.

Mast Feeders.—One source of food on the area which should not be overlooked is the very large harvest of acorns which has been produced each fall. For three seasons this was one of the most abundant and important fall foods. White oaks produced little, red oaks slighly more, and black oaks very large quantities. In addition to being the most frequent species the black oak bears an acorn that is small enough to be readily swallowed by pheasants and ducks; whereas the other two species are rather large to be used until they are opened by squirrels, stepped upon, or otherwise broken up.

During October and November much of the mast harvest disappeared through the activities of fox squirrels, which stored away large numbers of acorns in individual holes in the ground. Mallard ducks took most of the

FIG. 21. Wild bergamot upon which tree sparrows fed in February, 1936.

supply near the water, and other birds such as blue jays and pheasants were active elsewhere. The chipmunk (Audubon and Bachman, 1849; Kennicott, 1856; Cory, 1912; Howell, 1929) and white-footed mouse also use quantities of this food. Korstian (1927) observed that from 90 to 100 percent of the total yearly supply of acorns is sometimes taken by animals. Squirrels and mice were found to be particularly important in this respect. There is no evidence from the present work that competition for the acorn harvest is ever acute, although by analogy a small crop and the exhaustion of the supply in the fall might mean privation to the fox squirrel in late winter.

Food Relations of Carnivores

The more that is learned of the food habits of animals the more omnivorous most species are found to be. Thus ground squirrels are known to feed extensively upon insects (Gillette, 1889; Orcutt and Aldrich, 1892; Bailey, 1893; McAtee, 1925), while such structurally authentic carnivores as the raccoon and skunk consume quantities of fruits, mast, and grain (Dearborn, 1932; Hamilton, 1936a). In the following discussion several species are

treated which, though primarily herbivorous, have certain significant carnivorous habits that make it logical to include them here.

Carrion Feeders.—As a food carrion appears to be most significant at the time of the melting of winter snows. Then all of the diseased and subnormal animals that succumbed to winter weather are revealed, and the increased activity of skunks and opossums certifies that the supply will not last long. Skunks in particular have been found to be lean and evidently hungry after more or less inactivity and are capable of eating large quantities of carrion. In one case a skunk carcass was found to have been almost entirely eaten (by skunks) in one night. Such remains are usually trimmed by mice, which also eventually destroy the bones that are left. It appears probable that in spring this is the principal source of animal food for such rodents as require it; and the calcium furnished by bones may well be important to pregnant females. In the winter of 1936-37 carrion was not covered by snow and was taken at any time animals were active; but in the winter of 1935-36 the sudden melting of deep snow in February rendered very noticeable the intensive use of this food by the species indicated. Crows feed upon carrion habitually and consume most of the carcasses of animals killed on the highways.

At the poultry plant of the Kellogg Farm several thousand chickens are reared on open range each year. At night after the chickens are housed female skunks and their young are often found in the poultry yard eating the chickens that have died of disease and other causes. It is not to be doubted that this supply of carrion is on this area an important source of food for young skunks. Twelve box traps were set in the chicken range on the night of July 17, 1936. In the morning nine skunks and a barn rat had been caught, and one of the other traps was sprung.

Predators of Small Mammals.—The small mammal key industry of the Kellogg Farm consists principally of six species: the thirteen-lined spermophile, meadow mouse, prairie deer mouse, white-footed mouse, short-tailed shrew, and prairie mole. In addition to these are the chipmunk, Cooper lemming-vole, pine mouse, jumping mouse, least shrew, and cinereous shrew; but the latter species are of such infrequent occurrence that they are probably of little ecological significance. The cottontail rabbit may be included in the small mammal key industry, but it appears more logical to discuss the species with animals of larger size.

The mammalian predators of this key industry on the farm studied are the skunk, weasel, house cat, opossum, and short-tailed shrew. The two first mentioned are doubtless of greatest importance. That the skunk is a pertinacious destroyer of mice, particularly Microtines, has been attested to by nearly all of the investigators who have touched upon the subject (Richardson, 1829; Kennicott, 1858; Merriam, 1886; Seton, 1909; Cory, 1912; Nelson, 1918; Stone and Cram, 1920; Cuyler, 1924; Dixon, 1925; Hatt, 1930; Johnson, 1930; Dearborn, 1932; Goodwin, 1935; Hamilton, 1935, 1936b). A

series of 99 skunk stomachs from fall, winter, and spring was collected during the present study.[17] Of these, 38 were empty or contained only trap debris. Of the remaining 61 stomachs, 12 contained the remains of mice, all of which were Microtus. These rodents formed 44.5 percent of the contents of the 12 stomachs and 8.7 percent of the contents of the total series of 61. One stomach was from December, 3 from January, 1 from February, 4 from March, and 3 from April. In a report on 62 skunk stomachs (three species) Lantz (1923) found that small mammals were most commonly taken from January to March. In an examination of 414 fecal samples from May to September Hamilton found 14.1 percent small mammals which were chiefly mice. In field work on this area it was very evident from fecal specimens and signs that feeding upon small mammals began as soon as skunks were active in spring, and continued into the summer. In August and September insects (grasshoppers and beetles chiefly) formed the bulk of material in droppings and later fruits became important. The significance of the above facts is manifest when it is considered that rodent populations are at a minimum in late winter and spring, and thus predation at this season is most effective in limiting the yearly increase.

Skunk diggings have been very common in tunnels of the prairie mole, and a skunk has been found in the daytime eating the remains of a mole (possibly carrion). It appears likely that on this area skunks are an effective check on mole numbers.

As mentioned previously, weasels are most effectively adapted to preying upon small fossorial animals. They are persistent enemies of such mammals as chipmunks, spermophiles, and all species of mice. The latter fact is supported by observations on this area as well as by a large mass of evidence accumulated by many investigators (Richardson, 1829; De Kay, 1842; Audubon and Bachman, 1849; Kennicott, 1857; Rhoads, 1903; Fisher, 1908; Wood, 1910; Cory, 1912; Dearborn, 1932; Hamilton, 1933, 1935; Goodwin, 1935; Errington, 1936). Of 15 weasel stomachs taken on and near this area 9 were empty. In all of the remaining 6 were found the remains of mammals. One contained flesh and fur of Sylvilagus, 2 of Microtus, and 3 of Peromyscus. All appearances indicate that the weasel may be the most effective check on the numbers of the spermophile on this area. These ground squirrels are abundant and strictly diurnal. In the daytime they remain close to the burrow and appear to be very alert and watchful. Thus it is doubtful whether a large number are taken by avian predators, although their habits protect them not at all from weasels (Bailey, 1926; Seton, 1929). Few mammals are known to eat the short-tailed shrew, though Nichols and Nichols (1935) write of shooting a weasel that was carrying one. There is probably no species of small mammal on this area that is not, at least occasionally, preyed upon by this carnivore.

[17] I am indebted to Dr. Clarence Cottam, In charge, and Mr. E. L. Nelson of Food Habits, Division of Wildlife Research, U. S. Bureau of Biological Survey, for arranging for the analysis of these stomachs in the laboratory at Washington.

In the winter of 1935-36 under deep snow small mammals appeared to be well protected from house cats. In the following winter, when very little snow was present, cat tracks were often found in Microtus colonies in the fields. During the latter season 18 cat stomachs were collected on this area, of which 3 were empty. In the 15 which contained food, Microtus remains (and one Synaptomys) occurred in 12 and formed 31.1 percent of the food. Evidently cats hunted such prey regularly during this winter season. These animals are known to kill many species of small mammals (Forbush, 1916; Van Hyning, 1931), although most authors point out that they take them much less often than birds (Bailey, 1923; Couch, 1928; Hatt, 1930). To date not enough food studies have been made on the cat to warrant conclusions as to the extent to which the animal feeds upon small mammals. However on this area appearances indicate that natural predators such as the skunk, weasel, and some birds are of much more importance in reducing their numbers.

The opossum is very omnivorous and eats many kinds of plant and animal food (Rhoads, 1903; Cory, 1912; Seton, 1929; Dearborn, 1932). Although they doubtless destroy some rodents, the extent to which opossums feed upon carrion renders evidence from stomach analysis very questionable. Of this species 30 stomachs were collected, during the study, principally in fall and winter. In this series 3 were empty and 7 contained remains of mice (Microtus). In the 27 stomachs that contained food these mice constituted 6.4 percent. One of the stomachs contained remains of a short-tailed shrew, though this may well be carrion, as these animals are often found dead (Emmons, 1840; Evermann and Clark, 1911). Evidently opossums prey upon mice to some extent, although, as few are present on this area, they probably are not a very important factor in reducing populations of these rodents.

There is considerable evidence that the short-tailed shrew is an enemy of mice (Merriam, 1886; Shull, 1907; Hahn, 1909; Nelson, 1918; Bailey, 1923; Anthony, 1928). Johnson (1930) states, "The short-tailed shrew, where it is abundant, is more important in the control of mice than all other natural enemies of mice combined." However in 244 stomachs examined by Hamilton (1930) only 4 contained mouse remains. In the present study shrews have often been taken in Microtus colonies during the winter and, from the amount of food required by this species, mice may well be a considerable item in the diet at times when insects are relatively unavailable.

The avian predators of small mammals are so well known that no lengthy treatment is needed here. The predaceous birds on the area that are important as enemies of the key industry are the marsh hawk, red-tailed hawk, screech owl, and great horned owl. From its abundance and persistent hunting the marsh hawk is doubtless of greatest importance. Red-tailed hawks have been few in number and not always present. The two owls probably take a large yearly toll. That small mammals form the bulk of the food of these birds

has been shown by the extensive work of Fisher (1893) and numerous contributions by other investigators (Bird, 1929; Cahn and Kemp, 1930; Errington, 1932, 1933; Pearson, 1933). Useful summaries of other work are given by Baldwin, Kendeigh, and Franks (1932), May (1935), and Bent (1937). During the fall migration season rough-legged hawks were frequently seen hunting on the Kellogg Farm and in 1934 one of these birds was seen by Mr. F. F. Tubbs to settle onto a pole trap with a mouse *(Microtus p. pennsylvanicus)* in its talons. In February, 1937 a Cooper hawk was observed tearing at a grass nest of the field mouse, and an investigation disclosed three young mice in the debris. On two occasions great blue herons have been seen at close range to catch meadow mice, and have often hunted in grassy meadows where these rodents were plentiful. The hunting technique was the same as that used on frogs and appeared to be effectual.[18] Fisher (1908) has observed a similar relationship between herons and rodents. Crows have also often been seen in and around meadow mouse colonies and have doubtless taken their share. The work of Barrows and Schwarz (1895) and Kalmbach (1918) has shown that small mammals form a considerable portion of the food of crows. That a part of such food is carrion is very probable. Evidence is good, however, that much of it is the result of direct predation. Judd (1902) also refers to the destruction of small mammals by crows.

The enemies of small mammals include practically every carnivorous species on the area. Couch (1928) has observed that, in general, predatory birds are more effective in destroying rodents than predatory mammals. There is, in the present study, no entirely reliable evidence upon which to base a conclusion; however from the numbers of skunks, weasels, and cats present, as compared with the numbers of marsh hawks, screech owls, and great horned owls, it appears that on the Kellogg Farm predatory mammals have been the most potent controlling force.

Predators of Larger Mammals.—The larger mammals of this area are here considered to be the cottontail, fox squirrel, weasel, skunk, opossum, and cat. Only one species of predator appears to kill all of these animals—the farm dog. Dogs have not been listed as a part of the fauna of the area as they are present only incidentally. On a few nights in winter dogs evidently hunted the area, and one rabbit is known to have been killed. Doubtless such hunting occurred at other seasons, but it was seldom observed. The dog has here been considered a part of the human factor, a standpoint that has not seemed justifiable in the case of the house cat, which is habitually feral.

As an animal community the Kellogg Farm is dominated by the great horned owl. Although I am not aware that this bird has been known to kill adult cats, it has been found to include in its diet all of the other species listed as larger mammals. Its food habits were studied by Fisher (1893), Bird (1929), Errington (1932), and English (1934b). On this area only two

[18] In both cases where herons were seen to catch a mouse the animal was taken to water and immersed before being swallowed.

pellets were found. One contained the neck vertebrae and feathers of a black duck (the kill was also found) and the other consisted of rabbit fur and bones. Two more pellets from a woods a few miles away contained rabbit remains. One rabbit kill was examined that can probably be ascribed to the horned owl. It appears, from the evidence at hand, that this owl may be one of the principal natural factors that reduce the winter population of the cottontail on this area. Various reports indicate that the great horned owl is one of the few species that prey upon the skunk (Audubon and Bachman, 1849; Wilkinson, 1913; Seton, 1929; Goodwin, 1935). On this area only one kill was found that might have been owl work, and evidence in the case was very unsatisfactory. In view of the continuous field work that was being done and the lack of any further indications, it appears that not many skunks were taken during this study.

The red-tailed hawk is the largest diurnal bird of prey found on the farm discussed and may be listed as an enemy of the rabbit, squirrel, and weasel (Fisher, 1893; Errington, 1932; Pearson, 1933; English, 1934a, 1934b). Other works are cited by May (1935) and Bent (1937). In this study on one occasion a red-tail flushed from the ground was seen to be carrying a fox squirrel in its talons. The marsh hawk is the most numerous hawk on the area in summer and probably accounts for many young rabbits and possibly some adults. It has also been demonstrated that the crow takes numerous young of this species (Barrows and Schwarz, 1895; Judd, 1902; Kalmbach, 1918). Several raided rabbit nests have been found in this work that pointed toward the crow as a possible predator.

Of the larger mammals the rabbit is most often preyed upon by other mammals. One of its principal enemies on the Kellogg Farm is the house cat. In the winter of 1935-36 two adult rabbits were killed, with very good evidence that the predators were cats. One rabbit was killed and partly eaten by a cat in a funnel trap set for pheasants. In the spring of 1936 one cat in Midland Park is known to have brought in two young rabbits. In his comprehensive work on the domestic cat Forbush (1916) states that they are very active in the pursuit of young and old rabbits and that they also kill squirrels. Seton (1909) and Linsdale (1928) cite other records of rabbits having been killed by cats. Being ground foragers, the skunk and opossum doubtless take numerous nests of young rabbits, although many of the remains found in stomachs may be classed as carrion. Skunk diggings have been found in close approximation to raided rabbit nests on this area, and Cory (1912) and Cuyler (1924) have included young rabbits in the list of the skunk's food. Kennicott (1858) and Brayton (1882) state that skunks capture adult rabbits by catching them in burrows. That the weasel also kills adult rabbits in holes is indicated by statements of Audubon and Bachman (1849) and Kennicott (1857). Fisher (1908), Seton (1929), and Stone and Cram (1920) also list the rabbit as weasel food. Hamilton (1935) found rabbit remains to con-

stitute 13.1 percent of the contents of a series of 360 fall and winter stomachs from New York State. Dearborn (1932) found that rabbits formed 14.29 percent of the mammalian food in 37 Michigan specimens. Flesh and fur of a rabbit were present in one of 15 weasel stomachs collected in this work and examined in the laboratory of the Biological Survey. That weasels can catch young rabbits in the open is shown by an observation of Leopold (1937). There is little evidence to indicate how great a factor the weasel has been in reducing rabbit numbers on the farm studied. It is evident that these carnivores took large numbers of mice, which were plentiful and easily captured. As a result I suspect that the number of adult rabbits killed is small, although young rabbits may well pay a heavier toll. In summary, it may be said that rabbits have formed a considerable part of the basic food supply of the larger carnivores found on this farm and as such, in common with the smaller rodents, were an important quantity in the food economy of the area.

Predators of Birds.—In the present work few data have been obtained on the summer predators of birds. At this season cats are numerous and probably kill birds regularly. The marsh hawk may also take a share in summer; and when the great horned owl is present, avian food is doubtless a part of its diet. Crows are known to kill young birds and are common on the Kellogg Farm at this season. The above are probably the most important summer predators of birds, although there is almost no actual evidence. As elsewhere pointed out, good observations in summer on some phases of field research are comparatively rare.

In winter the great horned owl and Cooper hawk were the only resident avian predators of birds. All evidence indicates that the screech owl was not important in this respect. In two pellets of the horned owl from a perch a few miles from the farm were the remains of a cock pheasant. Numerous feathers scattered about showed that the bird had been carried to a stub to be eaten. In three years at least three of these owls were taken on or near the farm under conditions indicating that they had been killing young or full-grown chickens. One is known to have killed a black duck. Bird remains were common in the food specimens analyzed by Fisher (1893), Errington (1933), and English (1934b). In spite of this evidence, the black duck above referred to is the only wild bird known to have been taken by a horned owl on the farm. Rabbits and other rodents have been more numerous than pheasants and quail, and appearances indicate that they have been the main sustenance of these owls.

The most important winter predator of birds on the Kellogg Farm during this investigation was the Cooper hawk. During the first winter of the work two adult pheasants (one in a funnel trap) were known to have been killed by these hawks (fig. 22). In the second winter and spring four known pheasant kills by Cooper hawks were recorded and one case was observed that was questionable. On several occasions old remains were found after carrion

FIG. 22. A hen pheasant killed by a Cooper hawk in lowland brush cover.

feeders had performed their offices and it was not possible to judge as to the original predator. In the six cases enumerated above hawks were actually flushed from the kill. In one case a bird returned at least six times to a dead pheasant. Kills of other species that were found where evidence indicated this hawk, were a meadowlark, a junco, and a cardinal. When it is considered that by no means all of the kills on such an area as this can be found immediately and some not at all, it is evident that the Cooper hawk has been a real limitation to pheasant numbers. During the second winter no quail were on the area much of the time and no predation at all was recorded for this species during the study. It has been shown that the Cooper hawk lives primarily upon birds as food and is particularly destructive to pheasants and quail (Fisher, 1893; Baldwin, Kendeigh, and Franks, 1932; Errington, 1933; English, 1934b). Since from one to five of these birds were present at all times throughout both winters, from this fact alone it would appear probable that considerable mortality occurred among the winter birds of the farm.

Among the mammalian predators of birds the cat was, from observations, the most efficient. It is very doubtful that weasels ordinarily take many birds,

and the skunk and opossum are little inclined to prey upon adults; so that at the Kellogg Farm in winter the domestic cat appeared to be practically the only important enemy on the ground. In the first winter of the work a cat entered a funnel trap and killed and partly devoured a cock pheasant. A hen in the same trap dashed herself to death in fright. In the following winter a cat killed two wing-clipped Mongolian pheasants at the sanctuary and carried them into the pines to be eaten. There are, from this work, no known cases of cats having killed birds in the wild, although several old remains were found to which no cause could be ascribed (and which may also have been due to Cooper hawks). I have no doubt, however, that cats have taken numerous birds and very probably pheasants on this area. The many records of cat predation cited by Forbush (1916) and others (Bailey, 1923; Hatt, 1930; Stoddard, 1931), as well as the consistent hunting by these animals in all kinds of weather, lend weight to this analogy.

Nest Predators.—The impacts of predators on bird populations through nest losses is one aspect of the predator-prey relations problem that can be studied, to some extent, quantitatively. The difficulty of evaluating an individual predatory species as a limiting variable to bird numbers makes it increasingly important that such a method be used on those parts of the problem that can be so treated.

In the spring and summer a fairly large number of mallard ducks nest around Wintergreen Lake and the swales on the sanctuary. In 1935 the history of 31 duck nests was followed and 11 of these were destroyed by predators. The losses could not be ascribed to individual species, as there were no reliable criteria by which to recognize the work of each. In the spring of 1936 a nest predation experiment was performed that was designed to indicate differences in the work of various predators. If the work of these animals could be recognized, the facts obtained could be applied to nests raided under natural conditions in the wild.

As population studies were in progress on the farm and it was not desirable to injure or kill any animals on the area, the study was made in the turkey marsh. Ten false nests of four or five hens' eggs each (incubator infertiles) were placed in a variety of cover situations. Around each nest were set four steel traps. The nest sets were run early every morning and were operated from March 19 to June 12—a total of 850 nest-nights. At first it was felt that, due to artificial conditions such as a scent trail to the nests and other factors which might affect predatory species differentially, the data gained could not be used quantitatively to indicate the relative amounts of nest destruction accomplished by each species. From the results, however, I believe that these factors were relatively unimportant. Stoddard (1931) came to the same conclusion with regard to predation on quail nests that were visited regularly in his studies. Nests that were checked frequently suffered no more from predators than those upon which few observations were made.

He states that in areas where human trails are frequent (as in the turkey marsh here referred to) ground predators probably do not habitually follow them.

In the trapping at nest sets the following animals were taken: 14 skunks, 9 crows, 8 fox squirrels, 5 opossums, 3 weasels, 3 blue jays, and 8 miscellaneous animals most of which were probably caught incidentally (a thrush, a turtle, etc.). Of these sets 29 were raided without the predator being identified, and 33 were disturbed with good evidence remaining as to the animal involved (fig. 28). Such evidence was hair in a trap, droppings, or very typical work on eggs. Of the cases which were identified on such a basis 9 were attributed to skunks, 15 to crows, 6 to squirrels, and 3 to opossums. For these four species of animals, then, the total cases of predation were: crow, 24; skunk, 23; squirrel, 14; and opossum, 8.

After comparing the shells of eggs eaten in certain proved instances of nest destruction, it was evident that in some cases the work of the four most important predatory species could be distinguished. Skunks commonly chewed a large hole in the shell, leaving the edge crushed and the membrane frayed. Well-defined tooth marks in eggs were relatively rare. Skunks usually scattered the egg shells from a nest out on one side for a distance of from 10 to 20 feet (fig. 24). Opossums have been found to munch up eggs, leaving the shells completely crushed. Opossum work could not, however, always be separated from skunk work. In the eight observed cases of opos-

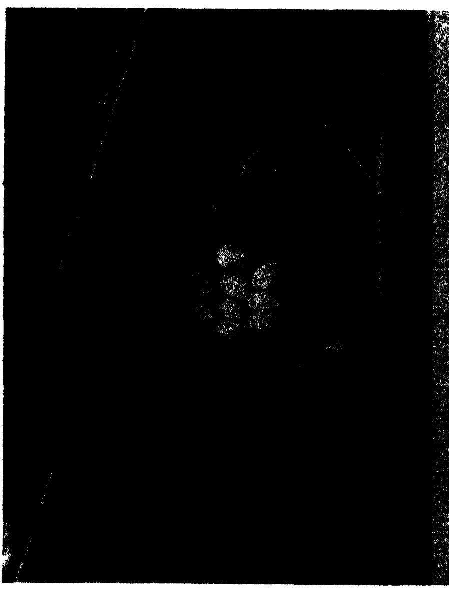

FIG. 23. Nest of mallard duck in lowland brush as it appeared on April 22, 1936.

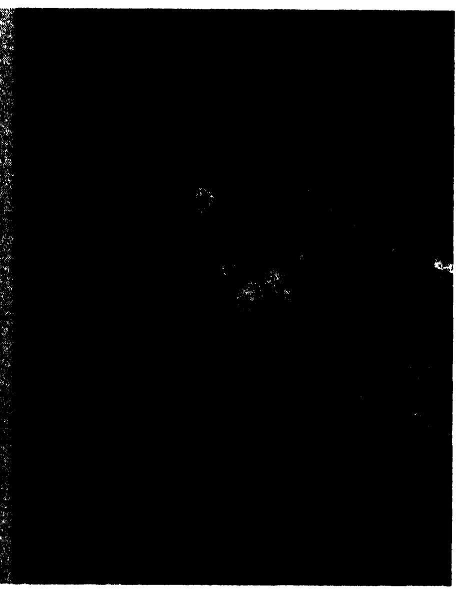

FIG. 24. The same nest as in fig. 23, on April 26, after being raided by a skunk.

sum predation the eggs were eaten in or within a few feet of the nest. Crows may split a cap neatly off one end of an egg (fig. 25), leaving no ragged edge or frayed membrane; or they may cut a groove or hole in one side. In the latter case the edges may be punched in, but are not crushed and ragged as in skunk work. Crows usually are unable to remove all the contents of an unincubated egg. They may also carry eggs away to be eaten elsewhere. Fox squirrel work was most typically represented by a neat cup left with the edges trimmed smooth and the contents licked out clean. The shells were usually left at the base of a tree (fig. 27) or on a stump. Shells left by squirrels and crows were sometimes similar.

It is to be emphasized that little can usually be inferred from a single egg. When an entire nest of eggs is eaten, however, their position noted, and the vicinity examined for other signs, a very good case may result.

In the application of this information to nests in the wild, 29 duck nests were studied in the spring of 1936. Of these, 10 were raided by predators. Three cases were identified as crow work, 2 as skunk, and 5 were unknown. Of seven pheasant nests checked, only one was raided—probably by an opossum, though possibly by a skunk. In the spring of 1937 records were obtained on 32 duck nests.[19] Of these, 17 were broken up by predators. Evidence was good that at least four were taken by crows and three by skunks. In most other cases evidence was poor. During this season, however, grackles were

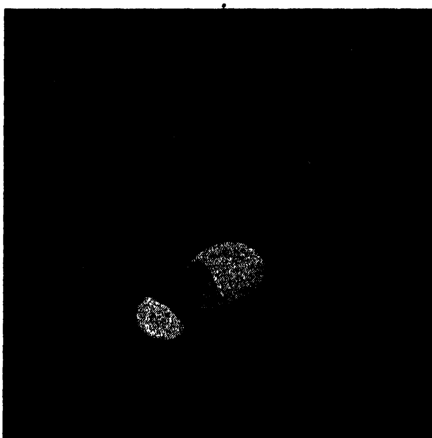

FIG. 25. A hen's egg after being eaten by a crow.

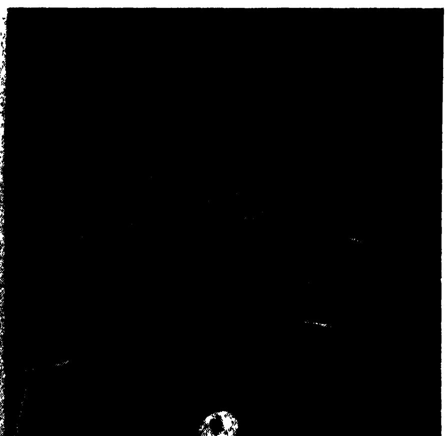

FIG. 26. A crow caught in steel traps at a false nest of hens' eggs.

[19] Most of the field work on this group of nests was done by Mr. Homer L. Bradley, who kept records and kindly called my attention to numerous cases of predation.

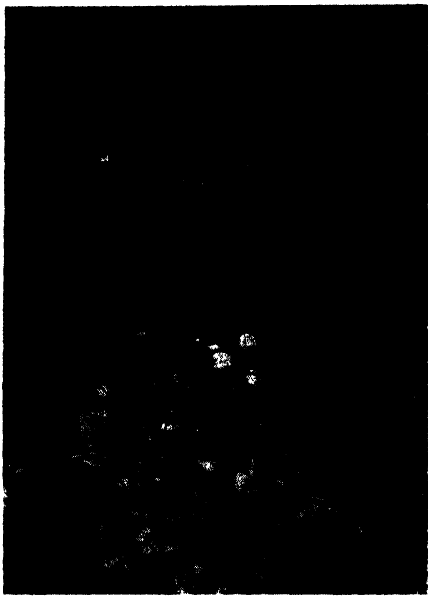

FIG. 27. Egg shells left at base of tree by a fox squirrel.

FIG. 28. A false nest raided by a skunk which escaped being caught but which left ample evidence of its identity. Arrow points to feces, which contained egg shells from a previous visit.

more numerous than usual, and several duck nests were found with some eggs that had small holes punched in them. It is very probable that these birds were responsible for a part of the losses, although there is little direct evidence. They were not known to have eaten eggs during the two years previous. Of a total of 99 nests (82 duck, 15 pheasant, 2 quail) observed in the wild during the three seasons 39 (38 duck, 1 pheasant) or 39.3 percent were broken up by predators. It is interesting to note that of 602 quail nests recorded by Stoddard (1931) 37 percent were destroyed by natural enemies. Hamerstrom (1936) found that 76.9 percent of 445 Iowa pheasant nests were unsuccessful, and that 19.3 percent of the losses could be attributed to predators. From the evidence available it appears that about one-third of the nests of ground-nesting birds were destroyed by egg-eating animals on the Kellogg Farm, and that such a rate of mortality may not be far from the usual loss suffered in such habitats. This can be more reliably judged when more data from other localities are available.

SUMMARY AND CONCLUSIONS

PURPOSE

The purpose of this study has been to demonstrate the approximate sizes and most vital interrelationships of the mammal and bird populations on 500 acres of farm land.

AREA

The area studied lies on an outwash plain in a recently glaciated region in southern Michigan. It includes Wintergreen Lake and five small kettle holes. The topography is somewhat irregular, varying between the 891- and 935-foot contours. About 277 acres have been cultivated.

In the order of their development in the hydrosere the plant habitats of this area may be listed as marsh, lowland brush, lowland woods, and upland woods. The stages of a secondary succession, starting with plowed ground, are also present here. The annual weed stage is found on cropland and, if undisturbed, will pass into the perennial weed and grassland stage. This, in time, becomes upland brush, which gives way to the upland oak woods.

This area resembles other surrounding farm land except for the ungrazed brush cover that has grown up in the lowlands and the coniferous plantings that have been made on the more hilly portions. An aggregate of about 20 acres of these plantings are present which vary in size from a few scattered trees to four acres of massed pines.

ANIMAL LIFE

The animal species of this area are discussed from the standpoints of abundance, habitat predilection, time of activity, and position in the food cycle. The summer and winter populations varied during the study to a marked degree owing to the fluctuation in numbers of resident animals and of migratory birds which were present during only a part of the year.

Population Studies

Censuses of mammals were taken principally by returns from trapping and marking. Winter burrow excavation was also used in the case of the skunk. Pheasants and quail were inventoried with bird dogs and by the interpretation of daily field work. Mice and shrews were taken in mouse traps baited with peanut butter. Quantitative studies have not been made on all species, and where figures are not available the comparative numbers present, as judged by indications, are given.

Rabbit.—Based upon the December kill and the number of individual rabbits trapped in January, February, and March the minimum population figure for December, 1935 was found to be 228. As judged by the number of individual rabbits taken in February and March the April population was about 25 pairs. In six weeks and five days, beginning on October 31, 1936, 102

rabbits were marked by trapping. On December 18, 19, and 20 a total of 126 rabbits were shot. Using the proportion of marked rabbits in the kill, the December population was calculated at 226 rabbits, or one animal per 2.1 acres.

Fox Squirrel.—In the fall and winter of 1935-36 sixty-one fox squirrels were marked by ear clipping. This constitutes an index population figure for about 30 acres of woodland (one squirrel per 0.49 acres). During the following summer the numbers of this species took a marked drop due, evidently to a mange-like disease that became epidemic. In the winter of 1936-37 only 39 individuals were taken.

Skunk.—During the first fall and winter 30 skunks were caught in the traps and marked. Of these, 20 were males. The sex ratio here is 0.5, and females are relatively inactive in winter. Hence if an equal number of females is presumed, the total number of skunks that are known to have used the area is about 40.

In the second fall and winter 29 male skunks and 15 females were taken in box traps. During the winter period of inactivity 19 burrows were excavated and two males and 16 females were handled that had not been taken in traps. Thus the total of skunks handled on this area was 62, or 31 males and 31 females. However, indications are that only 23 females occupied burrows on this area; and if there were an equal number of males, the total known resident winter population for the farm was 46 skunks, or one per 10.4 acres of land.

Ringneck Pheasant.—On a basis of bird dog censuses and daily field work the late fall population of 1935 was about 30 pheasants, or one bird per 16 acres.[20] In the following April the number was between 20 and 24. During the second winter many pheasants left the farm and gathered in a brushy area in the next section to the north. On January 22, 1937 only five pheasants were flushed in a census of the farm. Evidently numerous birds returned in the spring.

Bobwhite Quail.—Quail were censused in the same manner as pheasants. Populations were, however, even more variable due to movements. In December, 1935 the maximum number of bobwhite was observed when about 42 birls were on the area. Thus at this time the population density was about one quail per 11.4 acres. This species was much disturbed by the field work during the late winter period of deep snow. Evidently much shifting and splitting of coveys resulted from this factor. In the winter of 1936-37 a maximum of 10 quail were present and at times none at all was to be found.

Species of Lesser Abundance.—The winter weasel population, as judged by tracks, appeared to be about half a dozen individuals. On the same basis, from one to five cats were frequently on the area. The opossum population was small, evidently numbering three or four. In summer not more than two

[20] Population densities are calculated for 480 acres—Wintergreen Lake occupies 20 acres.

raccoons are known to have been present at one time, and there is only one fox record during this work. Woodchucks were uncommon on the farm, only three having been seen in three years. The winter Cooper hawk population evidently varied from one to five during two winters. The number of great horned owls was usually one and sometimes two.

Small Mammals.—Of the ground squirrels on the area the spermophile was abundant and the chipmunk comparatively uncommon. The most numerous small mammal was the prairie deer mouse, with the meadow mouse evidently second in numbers. The white-footed mouse, short-tailed shrew, and prairie mole were also common. Species of lesser importance were the star-nosed mole, masked shrew, least shrew, jumping mouse, Cooper lemming-vole, and pine mouse. The bulk of the small mammal key industry, then, was formed by the spermophile, prairie deer mouse, meadow mouse, white-footed mouse, short-tailed shrew, and prairie mole.

Animal Interrelations

Animal species interact chiefly by being associated in the same habitats and by being active at the same time. The most vital interrelationships arise through the necessity of every individual for food.

Habitat Relationships.—In summer herbaceous vegetation provides good cover everywhere and species like the cottontail, house cat, weasel, skunk, pheasant, and quail used nearly every part of the area. The fox squirrel and flying squirrel are restricted to woodland. The white-footed mouse was also found, but it includes brush areas and coniferous plantations in its habitat. In grassland the meadow mouse, spermophile, prairie mole, and prairie deer mouse were common, as were several species of sparrows and other birds. On cultivated ground the prairie deer mouse was the only permanent resident.

In winter the habitats of the squirrels, mice, and other species were the same as in summer except that meadow mice were often found in brush areas; and in the presence of snow, rabbits, pheasants, and quail were largely restricted to deciduous brush and conifers.

Activity Relationships.—The cottontail, fox squirrel, house cat, weasel, pheasant, and quail are designated predominants as they are active throughout the year. Among the smaller animals the prairie deer mouse, white-footed mouse, meadow mouse, and short-tailed shrew were the most common predominants. A large number of migratory birds were present only in summer and the raccoon was also found on the area studied only at this season. Resident animals that were active in summer but inactive during at least the coldest part of the winter are the skunk, opossum, woodchuck, spermophile, chipmunk, and jumping mouse. Common winter birds that were absent in summer are the Cooper hawk, junco, and tree sparrow. The great horned owl was regularly present in winter but appears to be only occasional in summer. The latter season is the time of greatest activity as all resident species are

active, as well as a large number of migrant birds. In winter the migrants are absent and several species of resident mammals are inactive.

Food Relationships.—Food relationships have been most easily studied in winter. It is at this season that supplies diminish and competition becomes most severe. Among herbivores field mice and rabbits were found to be the most typical feeders upon herbaceous plants; and when this food was covered with snow they subsisted upon bark. Potentially these two animals compete for this food supply and affect other species by reducing cover. On the Kellogg Farm, however, the amount of brush present was so large that neither of these relationships was vital in the winter of 1935-36. Another source of winter food for herbivores is the fruits and seeds of common weeds. Conditions of deep snow reduce the supply and bring about intensive competition between winter songbirds, pheasants and quail, and seed-eating mice such as the prairie deer mouse and white-footed mouse. A food shortage occurred in February, 1936. Through their habit of storing seeds mice probably did not suffer; the flocks of songbirds left the area; and pheasants and quail subsisted on other foods. The shortage was of brief duration, as snows melted in late February and exposed a new supply.

The carnivores on this area that feed on small mammals are the great horned owl, screech owl, marsh hawk, red-tailed hawk, crow, skunk, house cat, weasel, and opossum. The short-tailed shrew may be added as an enemy of mice.

The rabbit is the most important prey species among the larger mammals. It is taken by the horned owl, red-tailed and marsh hawks, crow, cat, skunk, weasel, and opossum. The fox squirrel is preyed upon by the red-tailed hawk, cat, and possibly the great horned owl and other species. The horned owl appears to dominate the community as it preys upon the skunk and thus utilizes larger food than any other predator on the area.

* * * * *

It is evident from this study that relatively dense populations of three species of large mammals have existed here together. The cottontail rabbit, the skunk, and the fox squirrel are abundant, and there is no apparent reason why they should not continue to thrive. Six species of small mammals are also particularly plentiful. The spermophile, prairie deer mouse, meadow mouse, white-footed mouse, short-tailed shrew, and prairie mole evidently find this farm a very favorable habitat.

Among birds the number of pheasants is low. The species has been conspicuously preyed upon by the Cooper hawk, but perhaps no more here than elsewhere. The drop in numbers from late fall to spring has been less than one-third, but the productivity of the breeding stock has been low. Evidently about one-third of the nests of pheasants are broken up by natural enemies. It is, however, not certain that the status of the bird can be attributed in any large measure to this factor, as such a proportion of nest losses may occur

even in favorable areas. The exact ways in which this environment is limited for pheasants have not been definitely established.

The large amount of cover makes this farm favorable to pheasants, rabbits, and other species in severe winter weather. The area also has been prolific of natural food supplies which supported large numbers of winter songbirds and other animals. The flora is very favorable to herbivorous species and hence the large, though probably not abnormal, numbers of small mammals found here are to be expected. It follows from this that the carnivorous species dependent upon the latter should also find the farm a favorable habitat. This is notably so in the case of the skunk; and the numbers of the weasel, cat, marsh hawk, redtail, horned owl, crow, and other carnivores are apparently about "normal" for these species.

On this area of farm land we have, in general, copious food supplies and abundant cover. The animal populations are characterized by large numbers of rabbits, squirrels, and skunks, but small numbers of pheasants. A knowledge of the consistency with which these relative numbers do or do not occur on other areas will throw further light upon the extent to which each of these species tends to determine the status of others.

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APPENDIX

CHECK-LIST OF VERTEBRATES

All of the species listed here have been recorded in Section 8, Ross Township, Kalamazoo County, Michigan, and nearly all were taken during the period from September, 1935 to June, 1937. For completeness the vertebrate fauna of Wintergreen Lake has been included, although the study has not dealt with "cold-blooded" forms. A total of 16 species of fishes, 12 amphibians, 12 reptiles, 162 birds, and 25 mammals have been recorded.

CLASS *PISCES*

Amia calva Linne	Bowfin
Erimyzon sucetta kennerlii (Lacepede)	Western lake chub-sucker
Notemigonus crysoleucas auratus (Rafinesque)	Western golden shiner
Notropis cornutus frontalis (Agassiz)	Northern common shiner
Notropis heterodon (Cope)	Black-chinned shiner
Notropis h. heterolepis Eigenmann and Eigenmann	Northern black-nosed shiner
Hyborhynchus notatus (Rafinesque)	Blunt-nosed minnow
Ameiurus n. nebulosus (Le Sueur)	Northern brown bullhead
Amieurus n. natalis (Le Sueur)	Northern yellow bullhead
Perca flavescens Mitchill	Yellow perch
Poecilichthys exilis Girard	Iowa darter
Huro salmoides (Lacepede)	Large-mouthed bass
Apomotis cyanellus (Rafinesque)	Green sunfish
Helioperca macrochira (Rafinesque)	Bluegill
Eupomotis gibbosus (Linne)	Pumpkinseed
Helioperca x *Eupomotis*	Bluegill x Sunfish hybrid

CLASS *AMPHIBIA*

Ambystoma maculatum (Shaw)	Spotted salamander
Bufo americanus Holbrook	American toad
Bufo fowleri Garman	Fowler toad
Acris gryllus (LeConte)	Cricket frog
Pseudacris triseriata (Wied)	Swamp tree-frog
Hyla crucifer (Wied)	Spring peeper
Hyla v. versicolor (Le Conte)	Common tree-frog
Rana cantabrigensis Baird	Wood frog

Rana catesbeiana Baird	Bullfrog
Rana clamitans Latreille	Green frog
Rana pipiens Schreber	Leopard frog
Rana palustris Le Conte	Pickerel frog

CLASS *REPTILIA*

Coluber constrictor flaviventris (Say)	Blue racer
Lampropeltis t. triangulum (Lacepede)	Milk snake
Natrix s. sipedon (Linne)	Water snake
Thamnophis sauritis (Linne)	Ribbon snake
Thamnophis s. sirtalis (Linne)	Common garter snake
Sternotherus odoratus (Latreille)	Musk turtle
Chelydra serpentina (Linne)	Snapping turtle
Emys blandingii (Holbrook)	Blanding turtle
Terrapene c. carolina (Linne)	Box turtle
Graptemys geographica (Le Sueur)	Map turtle
Chrysemys bellii marginata (Agassiz)	Western painted turtle
Amyda spinifera (Le Sueur)	Soft-shell turtle

CLASS *AVES*

Gavia i. immer (Brunnich)	Common loon
Podilymbus p. podiceps (Linne)	Pied-billed grebe
Phalacrocorax a. auritus (Lesson)	Double-crested cormorant
Ardea h. herodias Linne	Great blue heron
Casmerodias albus egretta (Gmelin)	American egret
Butorides v. virescens (Linne)	Eastern green heron
Nycticorax nycticorax hoactli (Gmelin)	Black-crowned night heron
Botaurus lentiginosus (Montagu)	American bittern
Ixobrychus e. exilis (Gmelin)	Eastern least bittern
Cygnus columbianus (Ord)	Whistling swan
Branta c. canadensis (Linne)	Canada goose
Branta bernicla hrota (Muller)	American brant
Chen h. hyperborea (Pallas)	Lesser snow goose
Chen caerulescens (Linne)	Blue goose
Anas p. platyrhynchos Linne	Common mallard
Anas rubripes tristis Brewster	Common black duck
Chaulelasmus streperus (Linne)	Gadwall
Mareca americana (Gmelin)	Baldpate
Dafila acuta tzitzihoa (Viellot)	American pintail
Nettion carolinense (Gmelin)	Green-winged teal
Querquedula discors (Linne)	Blue-winged teal
Spatula clypeata (Linne)	Shoveller
Aix sponsa (Linne)	Wood duck
Nyroca americana (Eyton)	Redhead
Nyroca collaris (Donovan)	Ring-necked duck
Nyroca valisneria (Wilson)	Canvasback
Nyroca marila (Linne)	Greater scaup duck
Nyroca affinis (Eyton)	Lesser scaup duck
Glaucionetta clangula americana (Bonaparte)	American goldeneye
Charitonetta albeola (Linne)	Bufflehead
Erismatura jamaicensis rubida (Wilson)	Ruddy duck
Lophodytes cucullatus (Linne)	Hooded merganser

Mergus merganser americanus Cassin	American merganser
Cathartes aura septentrionalis Wied	Turkey vulture
Accipiter v. velox (Wilson)	Sharp-shinned hawk
Accipiter cooperi (Bonaparte)	Cooper hawk
Buteo b. borealis (Gmelin)	Eastern red-tailed hawk
Buteo l. lineatus (Gmelin)	Northern red-shouldered hawk
Buteo p. platypterus (Vieillot)	Broad-winged hawk
Buteo lagopus s. johannis (Gmelin)	American rough-legged hawk
Aquila chrysaetos canadensis (Linne)	Golden eagle
Haliaeetus l. leucocephalus (Linne)	Southern bald eagle
Circus hudsonius (Linne)	Marsh hawk
Falco peregrinus anatum Bonaparte	Duck hawk
Falco s. sparverius Linne	Eastern sparrow hawk
Perdix p. perdix (Linne)	Hungarian partridge
Colinus v. virginianus (Linne)	Eastern bobwhite
Phasianus colchicus torquatus Gmelin	Ringneck pheasant
Rallus l. limicola Vieillot	Virginia rail
Porzana carolina (Linne)	Sora
Gallinula chloropus cachinnans Bangs	Florida gallinule
Fulica a. americana Gmelin	American coot
Oxyechus v. vociferus (Linne)	Killdeer
Philohela minor (Gmelin)	American woodcock
Capella delicata (Ord)	Wilson snipe
Actitis macularia (Linne)	Spotted sandpiper
Tringa s. solitaria Wilson	Eastern solitary sandpiper
Totanus melanoleucus (Gmelin)	Greater yellowlegs
Totanus flavipes (Gmelin)	Lesser yellowlegs
Pisobia melanotos (Vieillot)	Pectoral sandpiper
Pisobia minutilla (Vieillot)	Least sandpiper
Micropalama himantopus (Bonaparte)	Stilt sandpiper
Larus argentatus smithsonianus Coues	Herring gull
Larus philadelphia (Ord)	Bonaparte gull
Larus delawarensis Ord	Ring-billed gull
Hydroprogne caspia imperator (Coues)	Caspian tern
Chlidonias nigra surinamensis (Gmelin)	Black tern
Zenaidura macroura carolinensis (Linne)	Eastern mourning dove
Coccyzus a. americanus (Linne)	Yellow-billed cuckoo
Coccyzus erythropthalmus (Wilson)	Black-billed cuckoo
Tyto alba pratincola (Bonaparte)	Barn owl
Otus asio naevius (Gmelin)	Eastern screech owl
Bubo v. virginianus (Gmelin)	Great horned owl
Strix v. varia Barton	Northern barred owl
Chordeiles m. minor (Forster)	Eastern nighthawk
Chaetura pelagica (Linne)	Chimney swift
Archilochus colubris (Linne)	Ruby-throated hummingbird
Megaceryle a. alcyon (Linne)	Eastern belted kingfisher
Colaptes auratus luteus Bangs	Northern flicker
Centurus carolinus (Linne)	Red-bellied woodpecker
Melanerpes erythrocephalus (Linne)	Red-headed woodpecker
Sphyrapicus v. varius (Linne)	Yellow-bellied sapsucker
Dryobates v. villosus (Linne)	Eastern hairy woodpecker
Dryobates pubescens medianus (Swainson)	Northern downy woodpecker

Tyrannus tyrannus (Linne)	Eastern kingbird
Myiarchus crinitus boreus Bangs	Northern crested flycatcher
Sayornis phoebe (Latham)	Eastern phoebe
Empidonax t. traili (Audubon)	Alder flycatcher
Empidonax minimus (Baird and Baird)	Least flycatcher
Myiochanes virens (Linne)	Eastern wood pewee
Otocoris a. alpestris (Linne)	Northern horned lark
Otocoris alpestris praticola Henshaw	Prairie horned lark
Iridoprocne bicolor (Vieillot)	Tree swallow
Riparia r. riparia (Linne)	Bank swallow
Stelgidopteryx ruficollis serripennis (Audubon)	Rough-winged swallow
Hirundo erythrogaster Boddaert	Barn swallow
Progne s. subis (Linne)	Purple martin
Cyanocitta c. cristata (Linne)	Northern blue jay
Corvus b. brachyrhynchos Brehm	Eastern crow
Penthestes a. atricapillus (Linne)	Black-capped chickadee
Baeolophus bicolor (Linne)	Tufted titmouse
Sitta c. carolinensis Latham	White-breasted nuthatch
Certhia familiaris americana Bonaparte	Brown creeper
Troglodytes a. aedon Vieillot	Eastern house wren
Telmatodytes p. palustris (Wilson)	Long-billed marsh wren
Cistothorus stellaris (Naumann)	Short-billed marsh wren
Dumetella carolinensis (Linne)	Catbird
Toxostoma rufum (Linne)	Brown thrasher
Turdus m. migratorius (Linne)	Eastern robin
Hylocichla mustelina (Gmelin)	Wood thrush
Hylocichla guttata faxoni (Bangs and Penard)	Eastern hermit thrush
Hylocichla ustulata swainsoni (Tschudi)	Olive-backed thrush
Hylocichla f. fuscescens (Stephens)	Veery
Sialia s. sialis (Linne)	Eastern bluebird
Regulus s. satrapa Lichtenstein	Eastern golden-crowned kinglet
Corthylio c. calendula (Linne)	Eastern ruby-crowned kinglet
Anthus spinoletta rubescens (Tunstall)	American pipit
Bombycilla cedrorum Vieillot	Cedar waxwing
Sturnus v. vulgaris (Linne)	Starling
Vireo flavifrons Vieillot	Yellow-throated vireo
Vireo olivaceus (Linne)	Red-eyed vireo
Vireo g. gilvus (Vieillot)	Eastern warbling vireo
Mniotilta varia (Linne)	Black-and-white warbler
Dendroica a. aestiva (Gmelin)	Eastern yellow warbler
Dendroica c. caerulescens (Gmelin)	Black-throated blue warbler
Dendroica coronata (Linne)	Myrtle warbler
Dendroica v. virens (Gmelin)	Black-throated green warbler
Dendroica fusca (Muller)	Blackburnian warbler
Geothlypis trichas brachidactyla (Wainson)	Northern yellowthroat
Setophaga ruticilla (Linne)	American redstart
Passer d. domesticus (Linne)	English sparrow
Dolichonyx oryzivorus (Linne)	Bobolink
Sturnella m. magna (Linne)	Eastern meadowlark
Agelaius p. phoeniceus (Linne)	Eastern redwing
Icterus galbula (Linne)	Baltimore oriole
Euphagus carolinus (Muller)	Rusty blackbird

Quiscalus quiscula aeneus Ridgway	Bronzed grackle
Molothrus a. ater (Boddaert)	Eastern cowbird
Richmondena c. cardinalis (Linne)	Eastern cardinal
Hedymeles ludovicianus (Linne)	Rose-breasted grosbeak
Passerina cyanea (Linne)	Indigo bunting
Spiza americana (Gmelin)	Dickcissel
Acanthis l. linaria (Linne)	Common redpoll
Spinus p. pinus (Wilson)	Northern pine siskin
Spinus t. tristis (Linne)	Eastern goldfinch
Pipilo e. erythrophthalmus (Linne)	Red-eyed towhee
Passerculus sandwichensis savanna (Wilson)	Eastern savannah sparrow
Ammodramus savannarum australis Maynard	Eastern grasshopper sparrow
Passerherbulus henslowi susurrans Brewster	Eastern Henslow sparrow
Pooecetes g. gramineus (Gmelin)	Eastern vesper sparrow
Junco h. hyemalis (Linne)	Slate-colored junco
Spizella a. arborea (Wilson)	Eastern tree sparrow
Spizella p. passerina (Bechstein)	Eastern chipping sparrow
Spizella p. pusilla (Wilson)	Eastern field sparrow
Zonotrichia l. leucophrys (Forster)	White-crowned sparrow
Zonotrichia albicollis (Gmelin)	White-throated sparrow
Passerella i. iliaca (Merrem)	Eastern fox sparrow
Melospiza l. lincolni (Audubon)	Lincoln sparrow
Melospiza georgiana (Latham)	Swamp sparrow
Melospiza m. melodia (Wilson)	Eastern song sparrow
Calcarius l. lapponicus (Linne)	Lapland longspur
Plectrophenax n. nivalis (Linne)	Eastern snow bunting

CLASS *MAMMALIA*

Didelphis v. virginiana Kerr	Virginia opossum
Scalopus aquaticus machrinus (Rafinesque)	Prairie mole
Condylura cristata (Linne)	Star-nosed mole
Sorex c. cinereus Kerr	Masked shrew
Cryptotis parva (Say)	Least shrew
Blarina b. brevicauda (Say)	Short-tailed shrew
Procyon l. lotor (Linne)	Raccoon
Mustela frenata noveboracensis (Emmons)	New York weasel
Mephitis nigra Peale and Beauvois	Eastern skunk
Vulpes fulva (Desmarest)	Red fox
Marmota monax rufescens Howell	Rufescent woodchuck
Citellus t. tridecemlineatus (Mitchill)	Thirteen-lined spermophile
Tamias striatus lysteri (Richardson)	Lyster chipmunk
Sciurus hudsonicus loquax Bangs	Southern red squirrel
Sciurus niger rufiventer (Goeffroy)	Fox squirrel
Glaucomys v. volans (Linne)	Eastern flying squirrel
Peromyscus maniculatus bairdii (Hoy and Kennicott)	Prairie deer mouse
Peromyscus leucopus noveboracensis (Fischer)	Northern white-footed mouse
Synaptomys c. cooperi Baird	Cooper lemming-vole
Microtus p. pennsylvanicus (Ord)	Eastern meadow mouse
Pitymys pinetorum scalopsoides (Audubon and Bachman)	Northern pine mouse
Ondatra z. zibethica (Linne)	Muskrat
Rattus norvegicus (Erxleben)	Norway rat
Zapus h. hudsonius (Zimmerman)	Meadow jumping mouse
Sylvilagus floridanus mearnsii (Allen)	Cottontail rabbit

TABLE 5. ABUNDANCE AND AVAILABILITY AS FOOD FOR BIRDS OF SOME FRUITS AND SEEDS IN THE WINTER, 1935-36

	Approximate Duration of Availability				
Fleshy Fruits	Nov.	Dec.	Jan	Feb.	Mar
Aronia arbutifolia (Red chokeberry) (3)*	—	—			
Aronia melanocarpa (Black chokeberry) (3)	—	—			
Celastrus scandens (Bittersweet) (2)	—	—	—	—	—
Cornus amomum (Silky dogwood) (1)	—	—			
Cornus candidissima (Gray dogwood) (1)	—	—			
Cornus florida (Flowering dogwood) (3)	—	—			
Cornus stolonifera (Red-osier dogwood) (1)	—	—			
Crataegus (Hawthorn) (2)	—	—	—		
Evonymus atropurpureus (Wahoo) (3)	—	—			
Ilex verticillata (Michigan holly) (3)	—	—	—		
Juniperus communis depressa (Ground juniper) (3)	—	—	—		
Lonicera caerulea (Mountain fly honeysuckle) (3)	—	—	—	—	
Lonicera japonica (Japanese honeysuckle) (3)	—	—	—	—	—
Malus coronaria (Wild crab) (3)	—	—	—	—	—
Parthenocissus quinquefolia (Virginia creeper) (2)	—	—	—		
Phytolacca americana (Pokeberry) (2)	—	—	—	—	
Polygonatum pubescens (Solomon's seal) (3)	—	—	—	—	
Prunus serotina (Wild black cherry) (2)	—				
Rosa sp. (Rose) (1)	—	—	—	—	—
Rhus copallina (Shining sumac) (1)	—	—	—	—	—
Rhus glabra (Smooth sumac) (1)	—	—	—	—	—
Rhus typhina (Staghorn sumac) (1)	—	—	—	—	—
Sambucus canadensis (Elderberry) (1)	—	—			
Smilacina racemosa (False Solomon's seal) (3)	—	—			
Smilax herbacea (Herbaceous smilax) (3)	—	—	—	—	
Smilax hispida (Hispid smilax) (3)	—	—	—	—	
Solanum carolinense (Horse nettle) (3)	—	—	—	—	
Solanum dulcamara (Bittersweet nightshade) (1)	—	—	—	—	
Solanum nigrum (Black-berried nightshade) (3)	—				
Sorbus americana (Mountain ash) (3)	—	—	—		
Symphoricarpos racemosus (Coralberry) (3)	—	—	—		
Viburnum acerifolium (Maple-leaf viburnum) (3)	—				
Viburnum lentago (Nannyberry) (3)	—	—			
Viburnum opulus americanum (High-bush cranberry) (3)	—	—	—	—	—
Vitis vulpina (Wild grape) (1)	—	—	—	—	—
Dry Fruits and Seeds					
Amaranthus graecizans (Tumbling pigweed) (2)	—	—	—	—	
Amaranthus retroflexus (Redroot) (1)	—	—	—	—	
Ambrosia elatior (Ragweed) (1)	—	—	—	—	
Arctium minus (Burdock) (1)	—	—	—	—	—
Bromus tectorum (Brome grass) (2)	—	—			
Carex sp. (Sedge) (2)	—	—	—		
Cephalanthus occidentalis (Buttonbush) (1)	—	—	—	—	—
Chenopodium album (Lamb's quarters) (1)	—	—	—	—	
Cuscuta pentagona (Dodder) (2)	—	—	—	—	—
Echinochloa crusgalli (Barnyard grass) (3)	—	—			
Echinocystis lobata (Wild cucumber) (3)	—	—	—		
Fraxinus americana (White ash) (2)	—	—	—	—	—
Lespedeza hirta (Bush clover) (3)	—	—	—		
Lychnis alba (White cockle) (3)	—	—			
Melilotus alba (White sweet clover) (1)	—	—	—	—	
Monarda fistulosa (Wild bergamot) (1)	—	—	—	—	
Monarda punctata (Horse mint) (3)	—	—	—		
Nepeta cataria (Catnip) (2)	—	—	—	—	
Oenothera biennis (Evening primrose) (2)	—	—	—		
Panicum capillare (Old witch grass) (2)	—				
Plantago aristata (Bracted plantain) (3)	—	—	—		
Plantago major (Common plantain) (1)	—	—	—		

*Relative frequency as judged by field observations: (1)-abundant; (2)-common; (3)-less common.

TABLE 5. *(Continued)*

FLESHY FRUITS	Approximate Duration of Availability				
	Nov.	Dec.	Jan	Feb.	Mar.
Poa pratensis (Kentucky bluegrass) (1)	—	—	—		
Polygonum acre (Smartweed) (3)	—	—			
Polygonum coccineum (Water smartweed) (2)	—	—			
Polygonum convolvulus (Black bindweed) (2)	—	—	—	—	
Polygonum hydropiper (Water pepper) (2)	—	—			
Polygonum orientale (Prince's feather) (3)	—	—			
Polygonum persicaria (Lady's thumb) (1)	—	—			
Polygonum sagittatum (Arrow-leaved tearthumb) (1)	—	—			
Polygonum scandens (Climbing false buckwheat) (2)	—	—	—	—	—
Prunella vulgaris (Self heal) (2)	—	—	—	—	
Quercus alba (White oak) (2)	—	—			
Quercus borealis maxima (Red oak) (1)	—	—			
Quercus velutina (Black oak) (1)	—	—			
Robinia pseudo-acacia (Black locust) (3)	—	—	—	—	
Rumex acetosella (Sheep sorrel) (1)	—	—			
Rumex altissimus (Tall dock) (3)	—	—	—	—	—
Rumex crispus (Curled dock) (2)	—	—	—	—	—
Rumex obtusifolius (Broad-leaved dock) (2)	—	—	—	—	—
Rumex verticillatus (Swamp dock) (3)	—	—	—	—	—
Setaria lutescens (Yellow foxtail) (1)	—				
Setaria viridis (Green foxtail) (3)	—	—			
Steironema ciliatum (Fringed loosestrife) (3)	—	—	—		
Verbena hastata (Blue vervain) (2)	—	—	—	—	
Verbena urticaefolia (White vervain) (2)	—	—	—	—	

THE STRUCTURE AND DEVELOPMENT OF OLD FIELD SHORTLEAF PINE STANDS AND CERTAIN ASSOCIATED PHYSICAL PROPERTIES OF THE SOIL[1]

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CONTENTS

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THE STRUCTURE AND DEVELOPMENT OF OLD FIELD SHORTLEAF PINE STANDS AND CERTAIN ASSOCIATED PHYSICAL PROPERTIES OF THE SOIL

INTRODUCTION

Since the publication of Cowles' (1899) epochal work on the developmental nature of the plant communities of the Lake Michigan sand dunes, there have been countless studies of plant succession. Although successional studies have been carried on in almost all countries, this phase of ecology has been the particular province of the American workers led by such exponents of the dynamic theory of change as Clements, Cooper, Nichols, and others. Of necessity, many of the conclusions have been based on purely observational rather than quantitative data and have largely concerned only the changes in the vegetation itself. A few investigations have been made on the successional relations of such habitat factors as hydrogen-ion concentration, evaporation, and soil moisture.

European investigations have long been directed toward exact quantitative information concerning the vegetation of existing plant communities. In an attempt to explain the "raison d'être" of such communities, an intensive study of the environment, the edaphic phase in particular, has developed in conjunction with these quantitative vegetational analyses. It is only within the last few years that such studies have become prominent in American literature.

In the Piedmont region of North Carolina, much abandoned agricultural land is reverting to forest. In the early stages of this succession, pine is an almost universal dominant. This old field pine is very important economically and a quantitative knowledge of the mutual effects of pine vegetation and soil, during succession, would be of importance not only from a purely ecological standpoint but might also have many applications in the field of silviculture. With this in mind, detailed investigations of the vegetation and the soil were made on an old field successional series of shortleaf pine (*Pinus echinata* Mill.) stands in the Duke Forest in Durham County, North Carolina. The present study, then, is an attempt to apply quantitative phytosociological methods of vegetational analysis to the communities in a successional series and to correlate statistically these results with exact measurements of habitat factors, namely, certain physical properties of the soil.

HISTORICAL REVIEW

As has been previously pointed out, relatively little work has been done on the interrelationships between the physical properties of soil and the

change in vegetation during succession. For the most part, the investigations have been confined to the changes in the chemical make-up of soil as influenced by plant cover and the resultant effect on type of flora. The greater part of the work in this latter category has been confined to the change in the hydrogen-ion concentration of soil and its effect on the species present and on profile characteristics.

Schneider (1927), Griffith, et al. (1930), and others have shown that there is an increase in the acidity of the soil under pure pine stands with increasing age of the stand. This would undoubtedly be true also for the shortleaf pine stands in the Duke Forest, since Coile (1933) has found that the highly acid litter under shortleaf stands in the Forest increases the active acidity in the underlying mineral soil. It would seem reasonable then that the active acidity in the mineral soil would increase with age of stand due to the addition of the products of pine litter to the soil.

It has been demonstrated that this highly acid condition of litter causes a podsolized soil to develop under pine stands in climatic mull regions due to excessive leaching of iron and aluminum sesquioxides (Fisher, 1928; Stickel, 1928; Griffith, et al., 1930). Aaltonen (1928) has shown that this greater amount of leaching under forest stands, as compared to open fields, also tends to wash the available calcium and phosphoric acid deeper into the soil. He also found that, as a result of leaching, there was a slightly lower percentage of the smaller soil fractions in forest soils than in those of open fields.

In 1849, Jules Thurmann suggested that the physical factors of soils are far more important in relation to plant growth than are chemical properties. He believed that it is the physical structure of soil that regulates the distribution of species because of the interrelationships of structure and moisture conditions of soil. His theory has been subject to much discussion and, while it has its fallacies, it still holds true from the standpoint of forest soils. This greater importance of physical factors of forest soils over chemical constitution in regard to site quality has been stressed by Henry (1908), Kraus (1911), Toumey and Korstian (1937), and others.

While little has been published concerning the effect of vegetation on physical properties of soil during actual forest succession, there have been many investigations, mainly European, on physical differences between forested and cleared land. Outstanding contributions are those of Ramann (1897), Hoppe (1898), Albert (1912a, 1912b, and 1913), Engler (1919), Tschermak (1920), Burger (1922, 1929), Stewart (1932), and Auten (1933). Their results show that forest soils are much lighter and more porous than are those of cleared land. In a forest soil, the air capacity, water-holding capacity, and percolation rate tend to be higher, while volume-weight tends to be lower than in soil of any type of cleared land. These differences are mainly attributable to the greater number of root channels, more abundant soil fauna, and the large amount of accumulated organic matter under forest vegetation.

The recovery of these properties through revegetation has been relatively little investigated. Berkmann (1913) appears to have been the first to point out that soil structure was appreciably changed by the roots of plants growing in it. He found that this effect was greater in a clay soil than in a sandy type. In further studies he showed that meadow soils had a higher percolation rate than crop or barren soils because of the greater number of root systems. This effect of plant associations and their roots on soil, with special regard to plant succession, has been stressed by Meyer (1922). He emphasized the importance of the earlier stages in succession in the preparation of soil for plants which invade later and those which eventually make up the climax community. The pioneer plants tend not only to add humus to soil but their root channels give the soil better aeration. Auten (1933) says that a large degree of soil porosity was found to be regained 20 to 25 years after plantations of forest trees had been established on cultivated lands.

In central Europe, Aichinger and Siegrist (1930), studying air capacity of soil in relation to succession, pointed out that the appearance of the assembly of plants such as Convallaria, Maianthemum, Paris, and Oxalis on the floor of mixed forest was accompanied by an increase in air capacity of soil from 8 to 23 percent. The use of such herbaceous plants to indicate the physical nature of the forest soil is the basis of the Finnish forest type classification (Cajander, 1926). More recent work on the indicator value of certain plants in expressing the development of physical properties of forest soil has been produced by Berger (1934) and Gassert (1936).

While the quadrat method has been used many times in quantitative studies of vegetation during succession, such data have been subjected only rarely to a statistical phytosociological analysis. Dziubaltowski's (1918) investigation of the succession following the cutting of the Quercus-Carpinus forest in southern Poland is one of the few examples of this type of work. Dziubaltowski used the floristic-statistical methods of Jaccard (1902) and came to the conclusion that Jaccard's frequency curves best expressed the trend of succession. Braun-Blanquet and Jenny (1926) used the statistical phytosociological methods of Braun-Blanquet and Pavillard (1925) in working out the development of vegetation and soils in the central Alps. Among American workers who have applied phytosociological methods to the analysis of succession are Cooper (1922) in New England and Cox (1933) on alpine succession in Colorado.

PLAN OF STUDY

In any study of succession involving long periods of time, a great many of the conclusions must be reached by inference, that is, comparing areas of similar topography, climate, and soils in different stages of vegetative development. This method necessitates the choosing of comparable locations for investigation; stations which would be practically identical as regards the strictly physical factors of environment if there were no plant coverings.

It was planned to study the interrelationships of vegetation and physical factors of soil throughout the pine stage of old field forest succession and, for the reasons stated above, on areas as identical in physical environment as it is possible to find in nature. Climate (macroclimate) was first eliminated as a variable by limiting the stands to a very small part of Durham County, North Carolina. Specifically, the stands were located in the eastern portion of the Durham Division of the Duke Forest within an area of approximately 1.3 square miles. It is included within a rectangle of which the boundaries are State Highway 751 on the north, Sand Creek on the east, Cornwallis Road on the south, and Rigsbee and Erwin Roads on the west. Korstian and Maughan (1935) have described the climate of the Duke Forest, including the area under investigation.

The area lies wholly in the Durham Triassic Basin, the soils of which are quite varied. The majority are derived from sedimentary Triassic sandstones, mudstones, and shales, while a few are developed from igneous dikes and sills. In order to eliminate the variability of soils as a factor, it was decided to confine the problem to a single soil type if possible. Being least frequently eroded, the Granville sandy loam was selected from available types as being the most desirable for this study. According to Perkins, et al. (1924), Granville sandy loam has a grayish or yellowish surface soil and a subsoil of yellow or reddish sandy clay to clay. It is derived from the sandstones, mudstones, and shales of Triassic age and is often found surrounding igneous dikes and sills.

The topographical factor was minimized by selecting only those stands which were on level or nearly level areas. In several of the stands there was a slight slope, in all cases toward the south.

With the strictly physical factors of habitat being thus delimited to practically level areas of Granville sandy loam within a region of approximately one square mile, the next problem was to find a series of pine stands on these areas, ranging from recently abandoned cultivated lands with a few scattered seedlings to mature pine with a good undergrowth of hardwoods. To eliminate the effects of uneven stocking or partial cutting on physical properties of soil (Burger, 1927), only fully stocked stands which had been almost entirely free from cutting were considered. Since Lönnroth (1925), Von Pöntynen (1929), and Aaltonen (1934) have all pointed out that in pure coniferous stands there is a higher stem count of dominants on the better sites and a correspondingly low count of undergrowth, the present work was confined to the stands of better site quality in order to eliminate any error in density of vegetation due to inequalities in site. The site indices for shortleaf pine in the stands finally selected ranged from 66 to 80. These are stated as the amount of height growth for the species in 50 years. They were determined by height measurements of the dominant trees by members of the Duke Forest staff. There are no available recorded indices for the younger

stands because such indices calculated from height of trees are not reliable for stands of the younger age classes. However, these stands are on essentially similar sites as is shown by the fact that the ratio between the amount of colloids in the B_1 horizon and the depth of surface soil is practically the same for these stands as it is for the older stands. This is based on the work of Haig (1929) and Coile (1935) who have shown that there is a definite correlation between these soil factors and site index.

After examining all the stands in the area, a series of eight locations, all meeting the above requirements, were selected. These ranged from a field, abandoned about 5 years, to a mature pine stand in which the dominants averaged 110 years of age. All of these stands were even-aged and had seeded in naturally on abandoned fields. The abandoned field used in the study was in the Andropogon stage of development (Oosting, 1933 and Crafton and Wells, 1934) and there were a few scattered shortleaf pine seedlings. The appearance of this field at the time of investigation is illustrated in Fig. 1. The seven pine stands were of the following ages: 9 years, 13 years, 21 years, 31 years, 56 years, 83 years, and 110 years. Interior views of the 13 year, 31 year, and 110 year examples are presented in Figs. 2, 3, and 4, respectively. Extensive search revealed that these stations are practically the only shortleaf pine stands on Granville soil in the western part of Durham County which are as yet little changed from the natural condition. The age of the stand is the average obtained from increment borings of ten dominant pines in each stand.

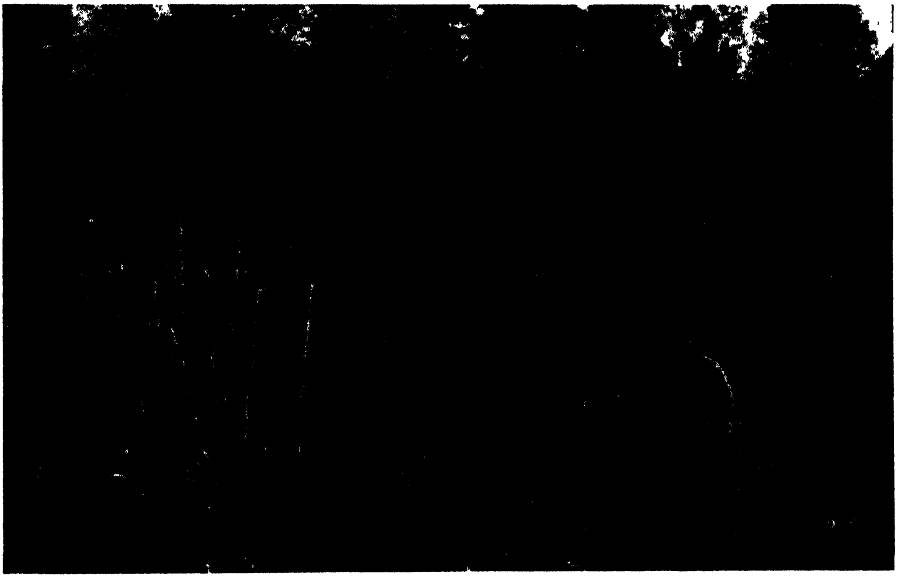

FIG. 1. The old field as it appeared at the time the study was made. *Andropogon virginicus* is the dominant.

Extensive search was made throughout Durham County for a young oak stand which had originated on Granville soil following shortleaf pine. It was thought that vegetational studies on the successor to the pine community

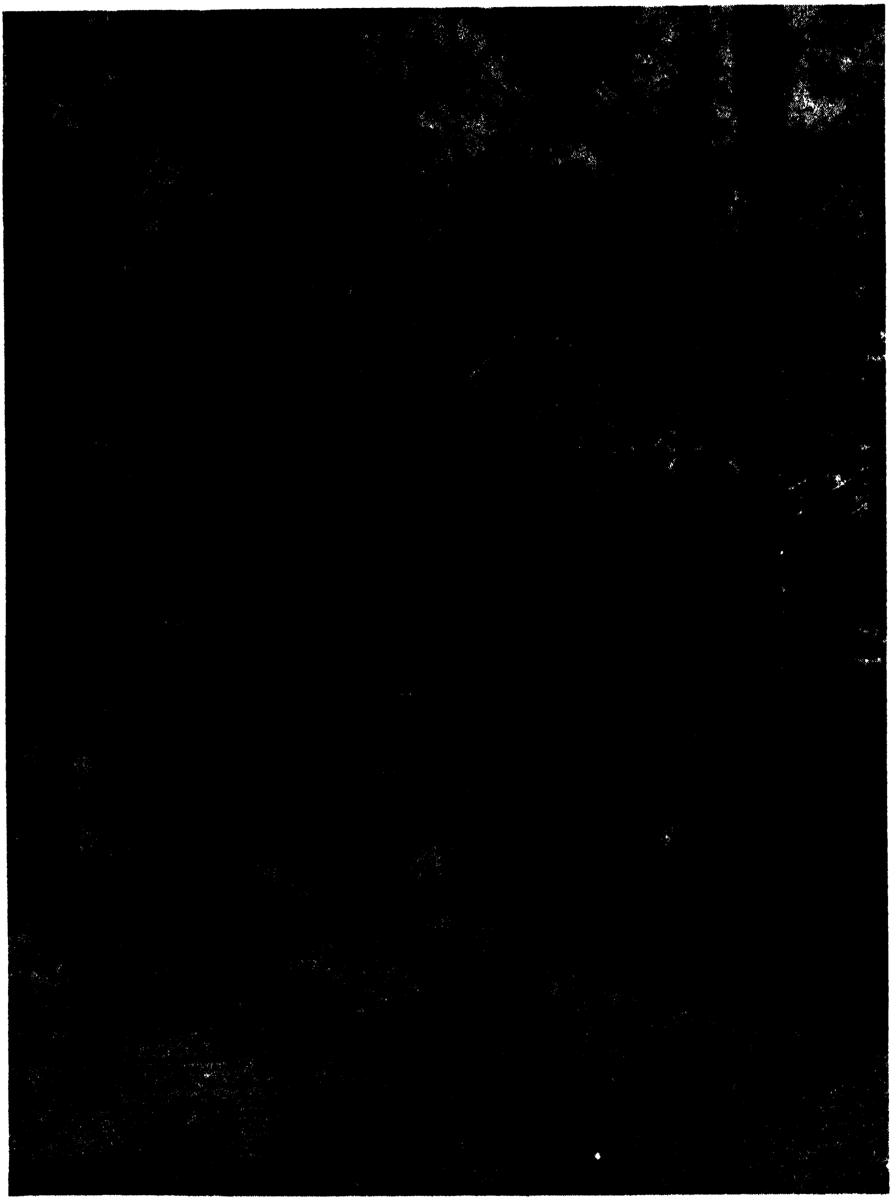

FIG. 2. An interior view of the 13-year old stand. Note the crowded condition of this stand and the already thick accumulation of needles on the ground.

might yield interesting results comparable to those found in New England by Fisher (1928) and Griffith, et al. (1930). Such a study might also throw some light on the question of climax communities of the Piedmont plateau.

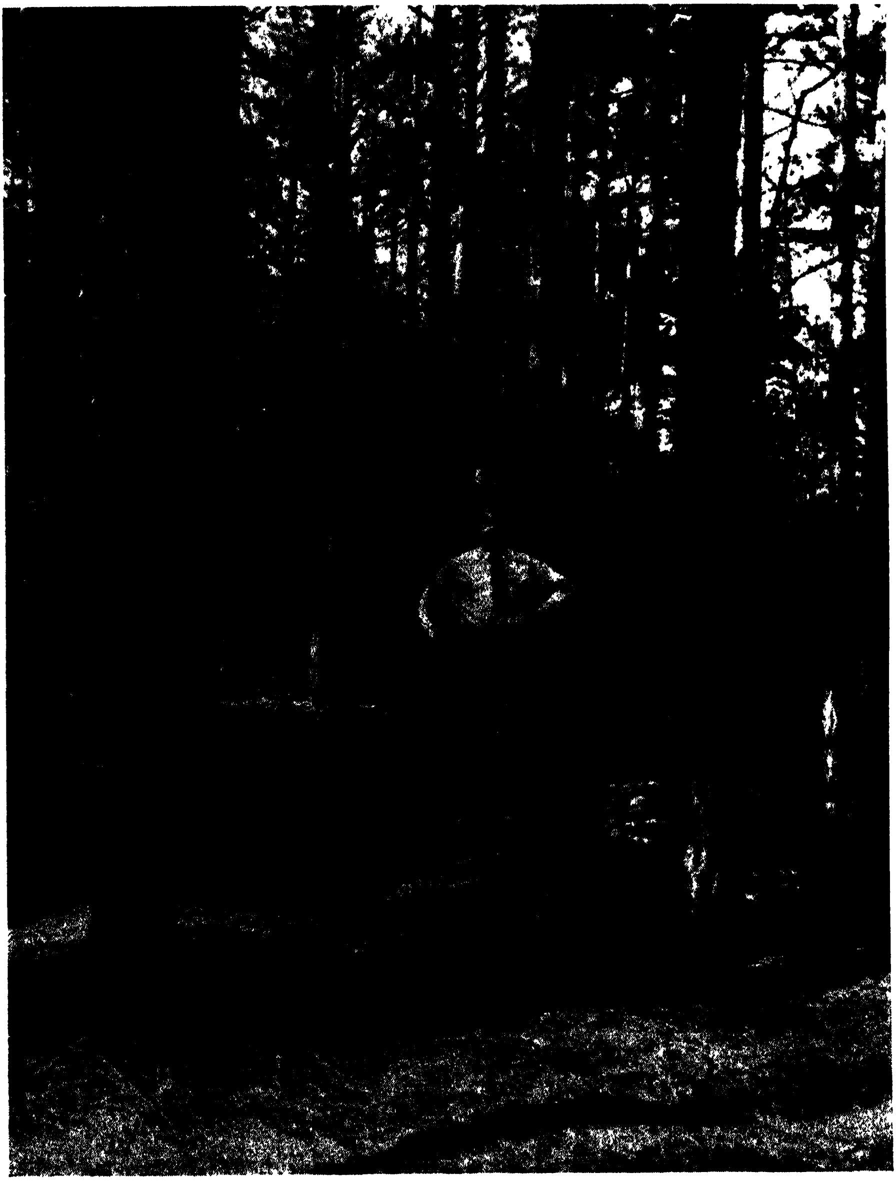

FIG. 3. An interior view of the 31-year old stand. Note that although the dominant pines are fewer than in the younger stands, the forest floor is quite barren of vegetation. Notice also the still-visible furrows as brought out by the undulating tree shadows.

The attempt was without success, however, as it seems that the Granville soils are much too important agriculturally to be given over to the growing of timber, especially the slowly growing varieties.

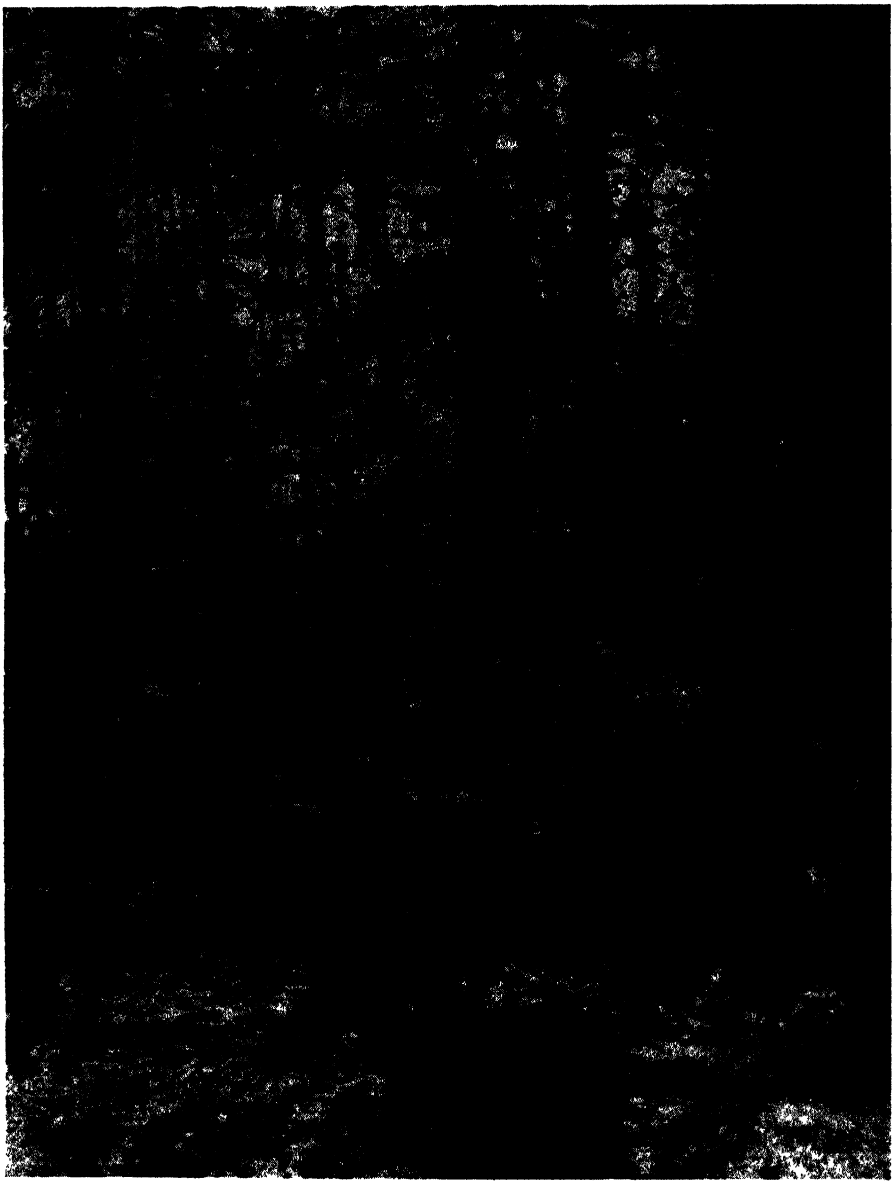

FIG. 4. An interior view of the 110-year old stand. The mature pines here are relatively far apart as compared to the younger stands and the forest floor is covered with a luxuriant undergrowth of young oaks and other hardwoods.

METHODS OF INVESTIGATION

VEGETATION

The vegetation of the various stands was studied quantitatively by the quadrat method. Count-lists were made for each vegetational stratum: the first being made up of the dominant, subdominant, and secondary trees; the second of the shrubs and woody reproduction; and the third of the herbaceous flora. As Cain (1934) has pointed out, size of quadrat is extremely important in such an investigation and the minimum area sampled in a community or in each stratum is dependent on the nature of that community or stratum. Among the methods for determining minimum quadrat size which Cain puts forth is the use of "percentage of total flora-to-area sampled" curves. In this procedure, the percentage encountered of the total species of the stand is plotted against the quadrat size or area sampled. The point at which the curve flattens most strongly is taken to be the minimum quadrat area. Cain worked only on the vegetation as a whole but he emphasized the fact that a separate investigation should be carried out for each vegetational stratum to determine the best quadrat size for that stratum.

With this in mind, a preliminary survey was made of the 110-year old stand to determine the size of quadrat which was most suitable for each layer. An intensive survey was first made of the whole area, which consisted of 4.62 acres, to compile a complete floristic list of the dominants, secondary trees, shrubs and "transgressives" (woody reproduction under 7 feet in height, Cain, 1934), and herbs. The first two strata were considered together because of the fact that practically the only dominant was pine and it was thought best to study pine and the secondary understory on the same quadrats for purposes of comparison. Ten sets of five quadrats each were distributed, widely and evenly, through this stand. In the same set, each quadrat included all the quadrats smaller than itself. The quadrats were of the following sizes: ¼ milacre, ½ milacre, 1 milacre, 4 milacres, and 25 milacres, with the smaller sizes being nested in one corner of the largest plot. A milacre is an area 6.6 feet on a side (0.001 acre) and was employed because of its extensive use by foresters.

Count-lists of dominant and secondary trees were made on all quadrats; of shrubs and transgressives on the four smaller sizes; and of herbs on the three smaller sizes. The results of this survey are shown in Tables 1, 2, and 3. Using the data included in these tables, species-area curves were plotted for each stratum. Hanson and Love (1930) and Cain (1934) suggest using the quadrat size at which a species-area curve breaks most strongly. Such a curve for the herbaceous flora breaks most strongly at the ¼-milacre size (approximately 1 square meter). This size was therefore adopted as being suitable for the herbaceous layer both from the standpoint of sampling and the amount of labor involved. Curves for the arborescent flora and for the

shrub and reproduction layer show breaks at the 4-milacre and ½-milacre sizes, respectively. However, in determining the frequency indices (Raunkiaer, 1918) on the various sized plots, it was found that on the 4-milacre quadrats, shortleaf pine, the only true dominant, had a frequency of only 40 percent. Furthermore, the most characteristic understory tree, *Cornus florida,* counted on the same quadrats had a frequency of only 70 percent on the 4-milacre quadrat size. These two species, both characteristic of the type of community, showed frequency indices of 80 percent and 100 percent, respectively on the 25-milacre or largest quadrat. It was thought best, therefore, in spite of the increased labor, to use the 25-milacre quadrat size for the arborescent strata, since the true distribution of the characteristic trees in the stand is more accurately shown by this size than by that size designated by the species-area curve.

TABLE 1. RELATION BETWEEN TOTAL NUMBER OF SPECIES IN ARBORESCENT STRATA AND SIZE OF SAMPLE PLOT

Area Sampled (Milacres)	Quadrat Size (Milacres)	Number of Species	Percentage of total flora of the stratum	Percentage of total stand area
2.5	0.25	4	16	0.054
5	0.5	6	24	0.108
10	1	7	28	0.216
40	4	14	56	0.865
250	25	21	84	5.411
4,620	Total stand of 4.62 acres	25	100	100

TABLE 2. RELATION BETWEEN TOTAL NUMBER OF SPECIES IN THE SHRUB AND TRANSGRESSIVE STRATUM AND SIZE OF SAMPLE PLOT

Area Sampled (Milacres)	Quadrat Size (Milacres)	Number of Species	Percentage of total flora of stratum	Percentage of total stand area
2.5	0.25	22	37	0.054
5	0.5	28	48	0.108
10	1	31	53	0.216
40	4	39	67	0.865
4,620	Total stand of 4.62 acres	58	100	100

TABLE 3. RELATION BETWEEN TOTAL NUMBER OF SPECIES IN HERBACEOUS STRATUM AND SIZE OF SAMPLE PLOT

Area Sampled (Milacres)	Quadrat Size (Milacres)	Number of Species	Percentage of total flora of stratum	Percentage of total stand area
2.5	0.25	16	44	0.054
5	0.5	19	52.7	0.108
10	1	22	61	0.216
4,620	Total stand of 4.62 acres	36	100	100

The same thing, as regards the inadequacy of the species-area curve when used alone, held true for the shrubby and transgressive stratum. Probably the outstanding characteristic of this layer in the older stands is the great amount of oak reproduction. The frequency of all the species of transgressive oaks taken together is only 70 percent on the ½-milacre size at which this species-area curve breaks most strongly. This frequency, however, reaches 100 percent on the 4-milacre quadrat size. So, in order to give a more accurate picture of the developing hardwood reproduction, the 4-milacre size was adopted for the study of this stratum.

As a result of the preliminary investigation, ten of each of the three quadrat sizes selected were laid out in each of the stands except the abandoned field, in which 20 ¼-milacre plots were distributed. The quadrats were arranged in sets of three quadrats with the smaller sized plots being included within one corner of the largest plot. These sets were distributed as widely and evenly throughout the stands as was possible. They were laid out by means of tapes, usually in two rows of five sets each, although in some cases this procedure varied with irregularities in the outlines of the stand.

Because of the fact that the preliminary work was done on the basis of ten plots of each size, this number was employed for the surveys of the other stands. Knowledge of the number of quadrats to use would be very appropriate in a study of this kind. The results obtained with ten quadrats of large enough size and evenly distributed seem to be adequate, however, for this problem.

Individual counts of all the species concerned were made for each quadrat. The data were analyzed to determine frequency (Raunkiaer, 1918) and density (Braun-Blanquet and Pavillard, 1925) of each species in each stratum of every stand. Some of the density data were correlated statistically with certain soil factors by the method of Wallace and Snedecor (1931). For the herbaceous and shrubby flora, the nomenclature of Small (1933) was followed. Sudworth (1927) was followed in the synonomy of the arborescent species.

SOILS

IDENTIFICATION AND LOCATION OF PROFILES

The soil under the stands was examined first with an auger and then a trench or soil well was dug in each stand to the depth of the C horizon for the purpose of identifying the soil by its profile and texture. This was done before any vegetational work was begun.

The trenches were approximately 6 feet long and 18 inches wide and ranged in depth from 3 to 6 feet. Similar wells were dug in other parts of each stand. These were always placed 3 to 5 feet away from a dominant pine so that comparable root data could be obtained. The number of trenches in a stand varied, four being the number in each stand except the 13-year and

83-year old examples in which three were dug. Because of the much lower number of roots and the almost total absence of tree roots, two wells were thought to be sufficient for the abandoned field.

ROOT STUDIES

At the time the ditches were dug, the face nearest the tree was smoothed off and the horizons and roots mapped. This was done with the aid of a string grid with intervals of 6 inches. The profiles were mapped 4 feet horizontally and 3 feet vertically on the scale of an inch to a foot. The roots were grouped into the five following size classes: 0.01 to 0.1 inch, 0.11 to 0.3 inch, 0.31 to 0.5 inch, 0.51 to 1 inch, and those over 1 inch were measured individually. The root data were analyzed as to percentage of roots in each horizon and also as to the percentage of roots in successive 6-inch depths from the surface. The percentages of the various size classes in each horizon and at each depth were also determined. Average thicknesses of the horizons were obtained from nine measurements for each horizon in the profile. The measurements were taken at intervals of 6 inches along the vertical lines of the grid.

ANALYSIS AND MEASUREMENT OF PROPERTIES

A composite sample of two quarts of soil was taken from the whole length of each horizon in the profile and brought into the laboratory where the soil was spread out on paper until thoroughly air-dry. Before the soil was subjected to analysis, it was put through a 2 mm. sieve to remove pebbles and roots.

Mechanical analysis of at least one profile in each stand was made by a modification of the Bouyoucos (1927a, 1927b, and 1928) hydrometer method. On the basis of the data obtained, the horizons were assigned to textural grades following the classification of Davis and Bennett (1927).

The moisture equivalent of the soils was determined by the method recommended by Veihmeyer, Oserkowsky, and Tester (1928). A preliminary investigation of one profile in each stand showed that the lower horizons in all stands were essentially similar in moisture equivalent value. Therefore, only the A_1 and A_2 horizons and the dark layer denoting the depth of plowing in the younger stands were more intensively worked.

The carbon and organic matter contents of the soils were determined by a modification of Schollenberger's (1931) method. The method is based on the oxidation of the carbon with a standard solution of chromic acid in sulfuric acid. The excess chromic acid is titrated against a standard ferrous ammonium sulfate solution and the amount of chromic acid reduced is then calculated. From this is determined the amount of carbon necessary to reduce the given amount of the standard chromic acid. Carbon has been found to make up approximately 58 percent of the organic matter in the mineral horizons of soil (Russell, 1932), so the carbon content in percent multiplied

by the factor 1.724 equals the percentage of organic matter. Loss on ignition, as a measure of organic matter, was determined on the samples from one profile in each stand. Determinations were made for organic matter on samples from the A_1, "plowed", and A_2 horizons from every profile and on those from the B_1 from one profile in each stand.

Samples were taken in undisturbed condition adjoining each soil well for the determination of volume-weight (apparent specific density), water-holding capacity, and air capacity. These samples were taken in undisturbed condition by means of the brass ring sampler described by Coile (1936). A trench was dug alongside the soil wells to collect the samples from the middle of the A_2 and B_1 horizons. Samples of the first 2 inches of surface soil were taken about 10 feet from the soil wells to avoid soil which had been disturbed during the digging of the ditches. It was found that the surface soil samples would often not hold together when the ring was used in the steel sampler. This was overcome simply by pushing the brass ring into the soil with the foot until it was full, care being taken not to compact the soil. The samples were trimmed of excess soil in the field and each end of the brass ring fitted with a copper lid.

In the laboratory, both lids were removed and a filter paper and a copper screen placed over one end. The samples were then immersed in water for at least 24 hours. At the end of this time, one lid was replaced and the cylinder turned over under water and removed. Excess water was wiped off and the sample weighed immediately. The cylinder was then turned over and with the screened end down, allowed to drain on paper towels for one hour and then re-weighed. The difference between the first and second weighings is a measure of the apparent air capacity. After the second weighing, the sample was dried in an oven at 105° C. for 48 hours and then weighed for the oven-dry weight. The soil was removed from the cylinder and the cylinder, screen, lid, and filter paper weighed. It was found that the circle of filter paper held about 2 grams of water, therefore, 2 grams were added to the weight of the cylinder, screen, and paper in the wet condition. The water-holding capacity of the soil is calculated from the amount of water held in the soil at the time of the second weighing. Allowing 1 gram of water as equal to 1 c.c., this is expressed as percentage of total volume of the sample (600 c.c.). The weight per c.c. of this known volume of oven-dry soil is the apparent specific density or volume-weight.

The data obtained from the soil investigations were subjected to statistical analysis to determine their reliability. Any determination exceeding three times the standard deviation from the mean was rejected and a new mean computed. In only one case was it necessary to do this. Simple correlation coefficients were calculated among the soil factors during succession by the method of Wallace and Snedecor (1931).

RESULTS OF VEGETATIONAL ANALYSIS

The results of the statistical study of vegetation are assembled in Tables 4 to 8 and in Figures 5 to 10. The tables show the frequency and density of each species encountered in the various vegetational strata studied. No statistical study of the "Bodenschicht" or moss layer was made since mosses and lichens are very infrequent in the stands under consideration. The density referred to is the average number of stems of a given species per unit area (Braun-Blanquet and Pavillard, 1925). Cain (1932b) defines the concept as, "abundance on a unit area basis". Frequency is a measure of the uniformity with which the plants of a given species are distributed throughout the community (Raunkiaer, 1918). It is usually expressed as the "frequency index" or percentage of quadrats in which the species appears rooted of the total quadrats of that size in the stand.

Table 4 shows the density and frequency of woody dominants and subdominants which were counted on the largest size quadrats (25 milacres). Shortleaf pine, the principal dominant, has a very high density of 71.6 per 25 milacres or 2,864 stems per acre in the 9-year age class. Some idea of this crowded condition in the young stands may be gained from Figure 2. As shown in Figure 5, the density of this species in the arborescent stratum declines rapidly in the succeeding age classes and then gradually levels off to a density value of 1.5 per 25 milacres or 60 stems per acre in the 110-year old stand. A frequency of 100 percent is maintained by this species up through the 56-year age class; this falls off to 90 percent in the 83-year stand and to 80 percent in the oldest stand. This decrease in number of dominant

TABLE 4. DENSITY (D) AND FREQUENCY (F) OF WOODY DOMINANTS AND SUBDOMINANTS

Species		Stand Age						
		9	13	21	31	56	83	110
Dominants								
Pinus echinata	d	71.6	50.6	30.9	12.8	6.3	3.8	1.5
	f	100	100	100	100	100	90	80
Pinus taeda	d	2.2	1.0	1.6	8	1		
	f	90	60	80	70	10		
Liquidambar styraciflua	d	.1					.2	
	f	10					20	
Diospyros virginiana	d	.2						
	f	20						
Juniperus virginiana	d	.4						
	f	40						
Liriodendron tulipifera	d				.1			
	f				10			
Quercus rubra	d						1	
	f						10	
Subdominants								
Liquidambar styraciflua	d							.3
	f							20
Oxydendrum arboreum	d							.1
	f							10

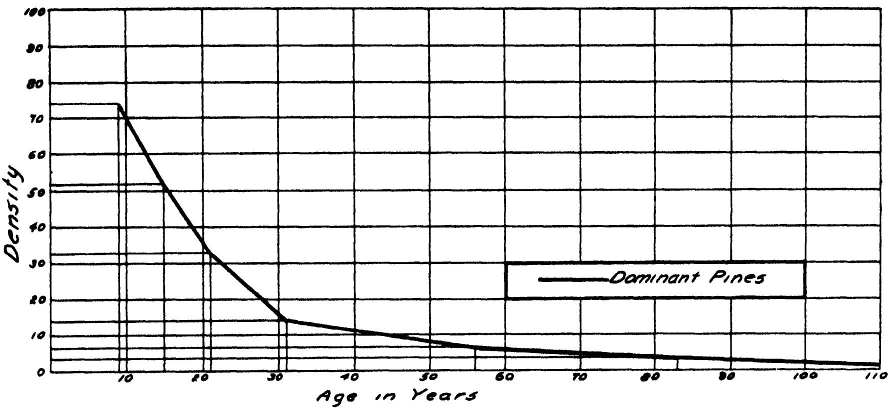

FIG. 5. Curve showing the decreasing density of the dominant pines from the 9-year stand to the 110-year stand. This curve is plotted from actual values.

stems and gradual opening of the stand is natural for a pure even-aged forest of pine which does not reproduce itself. The associated loblolly pine *(Pinus taeda)*, while never as dense as shortleaf pine, shows somewhat the same trend. It is almost negligible as a codominant after the stand is about 50 years old. The only other codominant found in more than one stand is sweet gum *(Liquidambar styraciflua)*. It seems occasionally to be an associate of the pine all through succession but in the stands studied, at least, is never very important. Red cedar *(Juniperus virginiana)* and persimmon *(Diospyros virginiana)* appear rather numerous as codominants in the 13-year stand but due to their slow growth, they are soon overtopped and never appear more important than secondary trees in older stands.

The secondary trees form a very definite layer society or synusia that becomes evident as the stand approaches middle age. In many stands it is quite distinct, especially in the spring when dogwood *(Cornus florida)*, redbud *(Cercis canadensis)*, and other conspicuous flowering trees are in bloom. Figure 9 shows this layer under an 85-year old pine canopy as it appears in early May with dogwood in bloom and other hardwoods coming into leaf. This stratum reaches a maximum height of about 35 feet but usually averages around 25 feet. Its flora is almost entirely broadleaved, the only exceptions being the two pine species, which soon disappear, and Juniperus which is fairly common all through succession. Dogwood is the most apparent species and also the one having the greatest density and frequency in this layer. It does not appear in any quantity or regularity as a secondary tree until the stand is between 40 and 50 years of age. From that time on, it is by far the most characteristic species in this layer. Two species occur in the secondary stratum in all stands. These are persimmon and tulip poplar *(Liriodendron tulipifera)*. The first shows no tendency to increase or decrease, merely holding its own, and never becomes more than 30 to 35 feet in height. The latter,

however, seems to be more numerous in older stands and it is possible that in some places, it might make up a part of the mixed deciduous forest which follows pine. Red maple *(Acer rubrum)* also seems to be quite important in older stands. It also shows a rather high amount of reproduction.

It is interesting to note that about middle age or between 50 and 60 years, several species of oaks begin to become important trees in the understory, this importance increasing in marked degree with increasing age of stand. Referring to Table 5, it can be seen that with the exception of tulip poplar, the oaks and hickories are the only potentially dominant genera which increase in number of individuals and also in extent of area covered through this particular type of succession.

Although the pine is still almost one hundred percent dominant in the mature stand, it is interesting to note in Figure 6 the comparison of the density and frequency of dominant and secondary hardwoods. As the density and frequency of the pines decrease, those values for the hardwoods increase, so that in the mature pine stand, the understory hardwoods have a density of over 13 times that of the pine and a frequency of 100 percent as compared with 80 percent for pine. It is very clear that as soon as one of the old dominant pines dies, the numerous hardwoods will quickly close the gap and the pine stand will be a step nearer the deciduous forest.

Probably the most interesting of the vegetational strata from the standpoint of succession is the shrub and "transgressive" layer. A detailed knowledge of reproduction in this stratum, coupled with an understanding of survival capacity of the various tree species, makes possible a fairly accurate prediction as to the future of the stand. The data concerning the secondary tree layer show to some extent survival capacity of an arborescent species. By combining the knowledge derived from this latter stratum with informa-

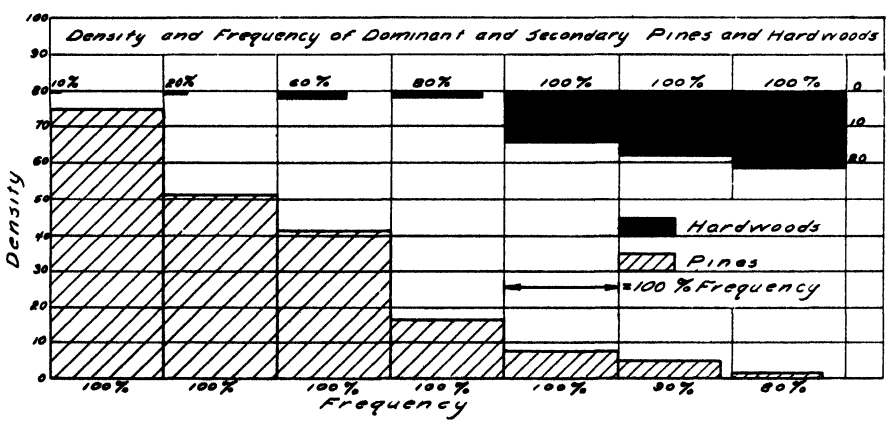

FIG. 6. The density and frequency of the dominant and secondary pines contrasted with the density and frequency of the dominant and secondary hardwoods throughout the succession. Note the increasing importance of the hardwoods and the steadily decreasing importance of the pines.

TABLE 5. DENSITY (D) AND FREQUENCY (F) OF SECONDARY TREES

Species		Stand Age 21	31	56	83	110
Pinus echinata	d	9 1	3.0	1.0	1.1	.1
	f	100	80	60	50	10
Pinus taeda	d	.1	1	.1		
	f	10	10	10		
Diospyros virginiana	d	2	9	.1	2	.2
	f	20	50	10	20	20
Liriodendron tulipifera	d	5	.4	1 0	8	2 0
	f	40	40	70	40	60
Platanus occidentalis	d	.1				
	f	10				
Sassafras variifolium	d	1.1				
	f	20				
Juniperus virginiana	d		1	4 0	4 7	1.5
	f		10	90	90	90
Oxydendrum arboreum	d		.1	1 9	1 5	9
	f		10	50	40	70
Acer rubrum	d			.8	5	3.4
	f			40	40	50
Cornus florida	d			7.1	8 2	7.8
	f			100	100	100
Fraxinus americana	d			1		
	f			10		
Hicoria glabra	d			.3		.4
	f			10		30
Liquidambar styraciflua	d			1 3	1 6	1 0
	f			60	80	50
Nyssa sylvatica	d			.2	.1	.2
	f			20	10	20
Ostrya virginiana	d			1	.1	
	f			10	10	
Quercus alba	d			1		1 6
	f			10		50
Quercus borealis var. *maxima*	d			4		1 3
	f			20		60
Quercus velutina	d			1	1 9	8
	f			10	90	60
Ulmus alata	d			1	3	.1
	f			10	20	10
Viburnum rufidulum	d			5		
	f			40		
Amelanchier canadensis	d				1	
	f				10	
Cercis canadensis	d				7	
	f				30	
Hicoria alba	d				.2	.5
	f				20	30
Quercus rubra	d				1 5	4
	f				90	30
Quercus stellata	d				4	
	f				20	
Styrax grandiflora	d				1	
	f				10	
Ulmus americana	d				.1	.1
	f				10	10
Fraxinus pennsylvanica var. *lanceolata*	d					.1
	f					10
Fraxinus pennsylvanica	d					1
	f					10
Morus rubra	d					.1
	f					10
Prunus serotina	d					.1
	f					10

tion concerning the amount of reproduction, it is possible to estimate the importance of a species as a future dominant.

The most striking feature in this lowest woody stratum is the rapid falling off and complete disappearance of shortleaf pine reproduction by the time the stand reaches 50 years of age. This is conclusive proof, when combined with the data on dominant and secondary pines, that the pine stage is ephemeral and eventually disappears because of its inability to reproduce under its own cover.

In sharp contrast to the amount of pine reproduction, is that of the hardwoods, especially the oaks. Figure 7 shows graphically the disappearance of

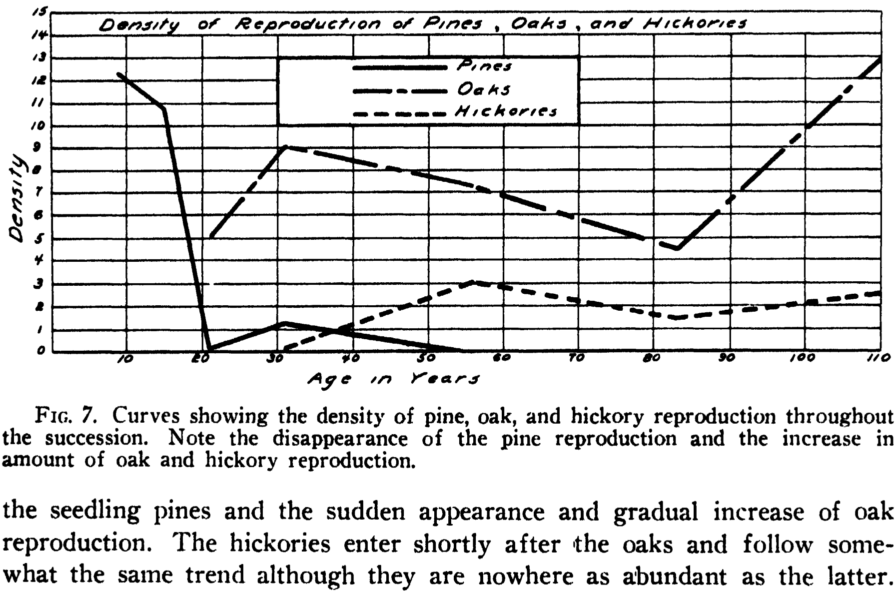

FIG. 7. Curves showing the density of pine, oak, and hickory reproduction throughout the succession. Note the disappearance of the pine reproduction and the increase in amount of oak and hickory reproduction.

the seedling pines and the sudden appearance and gradual increase of oak reproduction. The hickories enter shortly after the oaks and follow somewhat the same trend although they are nowhere as abundant as the latter. Combining this knowledge with what has been stated above concerning the abundance and frequence of oaks and hickories in the secondary layers of the older stands, it is safe to predict that in the deciduous community following shortleaf pine on these light-textured upland soils, these two genera will be foremost in importance. The species of oak most abundant in the younger stands is southern red oak *(Quercus rubra)*. It first makes its appearance as early as the 21-year stand and is very abundant both in that stand and in the 31-year stand. The other three species of oak *(Q. alba, Q. velutina,* and *Q. borealis* var. *maxima)* are much slower in becoming established. These three, however, all eventually become more abundant than *Q. rubra* in the oldest stand, with *Q. alba* being present in greatest numbers. These data show every indication that the eventual hardwood stand will approach the white oak-black oak-red oak cover type (Type 49) of the Society of American Foresters' Committee on Forest Types (1932).

The reproduction of red maple is interesting because of the fact that it is fairly abundant in every one of the pine stands and gradually increases in density with increasing age of stand. Its survival capacity under the pine cover is also good, as can be seen in Table 5. Because of its rapid development when grown in the open, it seems reasonable to predict that if the pine were cut, red maple would be one of the dominant trees in the hardwood stand immediately following cutting. However, in a stand which was not cut and the pines allowed to die out naturally, the more slowly growing oaks would have time to overtop the smaller red maple and the maple would remain as a secondary tree.

Among the other hardwoods, sweet gum *(Liquidambar styraciflua)*, which has fairly abundant reproduction in young stands, falls off in this respect in older stands and cannot be considered as a potentially important dominant following pine on these soils. The black gum *(Nyssa sylvatica)*, while nowhere very abundant, increases in both reproduction and in the secondary tree class with increasing age of the pine. This is probably due to a bettering of the moisture conditions since Nyssa tends to be a tree of moist places.

Dogwood, the tree showing the greatest amount of reproduction, is the most important tree of the secondary arborescent synusia. In the mature pine stand it shows a density of reproduction of 7,425 stems per acre and this combined with its 312 stems of secondary tree size per acre in the same stand, indicates the importance of this characteristic understory species. From the middle age classes of pine to maturity, it constantly increases its position as the most important secondary tree and it shows every indication of carrying this importance (as a secondary tree) over into the deciduous community. Observations on mature oak-hickory stands show that dogwood is apparently still the most characteristic understory tree and is still reproducing abundantly. As Lippmaa (1933) advocates and Cain (1934) suggests, this might be considered as an argument that, in some cases, layer societies or synusiae are separate communities in themselves being dependent on an overstory but entirely independent of the floristic composition of that overstudy. As Gleason (1936) has pointed out, this does not mean that such a synusia can be considered as a separate association because its individuals are in intimate association with the members of the other synusiae of the stand as regards the environmental factors. Thus, the stand is an intimate complex of several synusiae which may vary in themselves during the life of the stand or true association and if the association is successional, may even out-live the original association and become an integral part of its successor.

In the younger stands, the principal non-arborescent woody species is the trumpet vine *(Bignonia radicans)*. It is very abundant in some stands and entirely absent in others, but it seems never to be important in the oldest stands. A shrub characteristic of the pine forest is downy viburnum *(Viburnum rafinesquianum)*. It appears very abundantly as soon as the crown cover is

TABLE 6. DENSITY (D) AND FREQUENCY (F) OF WOODY TRANSGRESSIVES IN SHRUB LAYER

Species		Stand Age						
		9	13	21	31	56	83	110
Pinus echinata	d	12 3	10.8	.2	1.3			
	f	100	100	20	50			
Pinus taeda	d	.2		.1				
	f	20		10				
Acer rubrum	d	1 8	.8	.5	2 1	2.3	2 0	9.4
	f	80	40	40	80	80	80	100
Cornus florida	d	.2	.5	.4	5	13.3	13.4	29.7
	f	20	40	40	30	90	100	100
Juniperus virginiana	d	.3	.8	.2	1 1	2 5	3.1	6
	f	30	70	20	50	70	90	40
Liquidambar styraciflua	d	6.8	3 1		.6	.2	3.3	.5
	f	90	80		20	20	80	20
Liriodendron tulipifera	d	.3	7	.2	9	.4	1.5	.5
	f	20	60	10	30	30	60	30
Oxydendrum arboreum	d	1		.1			.2	1.0
	f	10		10			20	30
Platanus occidentalis	d	1						
	f	10						
Ulmus alata	d	.2	1			1	3	
	f	20	10			10	10	
Acer floridanum	d		3					
	f		20					
Crataegus sp.	d		.1		2	.1		3
	f		10		10	10		20
Prunus angustifolia	d		.1					
	f		10					
Ulmus americana	d		1	.2				
	f		10	20				
Viburnum rufidulum	d		.1	1	1	1.0	.1	2
	f		10	10	10	60	10	10
Amelanchier canadensis	d			1	.1	1 2		.7
	f			10	10	30		50
Celtis occidentalis	d			1		.1	.1	
	f			10		10	10	
Juglans cinerea	d			.1				
	f			10				
Prunus pennsylvanica	d			.1				
	f			10				
Quercus alba	d			2	.4	3.1	1.5	4.5
	f			10	40	90	70	100
Quercus phellos	d			.7		.2	.3	
	f			20		20	30	
Quercus rubra	d			4.0	7.8	2.5	1.5	2 7
	f			90	80	70	70	80
Quercus velutina	d			.2	1.5	1.1	1.1	2.9
	f			10	70	40	60	100
Sassafras variifolium	d			1.0	.7	2 5	.2	.8
	f			20	50	60	20	50
Ailanthus altissima	d				.1			
	f				10			
Diospyros virginiana	d				.5	7	1.2	.8
	f				30	40	60	50
Hicoria alba	d				.2	1.5	1.4	4
	f				20	50	70	30
Quercus borealis var. *maxima*	d				.4	.4	.1	2.9
	f				30	20	10	100
Fraxinus americana	d					1.1		
	f					10		
Hicoria cordiformis	d					.4		
	f					40		

TABLE 6. *(Continued)*

Species		Stand Age						
		9	13	21	31	56	83	110
Hicoria glabra	d					1 2	1	2.2
	f					50	10	90
Nyssa sylvatica	d					1	.5	3.0
	f					10	30	50
Ostrya virginiana	d					1	.1	
	f					10	10	
Viburnum prunifolium	d					.2	6	.2
	f					20	20	20
Cercis canadensis	d						.2	.3
	f						10	10
Morus rubra	d						1	.1
	f						10	10
Quercus stellata	d						1 1	
	f						30	
Fagus grandifolia	d							2
	f							10
Hicoria carolinae-septentrionalis	d							.2
	f							10
Ilex opaca	d							.2
	f							10
Prunus serotina	d							.2
	f							10

completely closed and is still fairly abundant in mature stands. Two woody vines, Virginia creeper *(Parthenocissus quinquefolia)* and muscadine grape *(Muscadinia rotundifolia)* form a very characteristic part of the shrubby flora of the older stands. Virginia creeper is present in the 9-year stand and becomes increasingly abundant as the pine reaches maturity. The muscadine grape, although not as abundant as Virginia creeper, shows an even more regular climb to its high density in the oldest stands.

As regards the herbaceous flora, the abandoned field is much richer than any of the pine stands. There is a gradual decrease in the number of herbaceous species until the crown is completely closed and from then on, the number of species remains fairly constant. However, Figure 8 shows that the herbaceous flora of the mature pine stand is almost entirely different floristically from that of the open field. Only two species, *Aster ericoides* and *Panicum sphaerocarpon,* are found in both locations. These are characteristic of the old field vegetation and occur in small openings in the mature stand.

The field vegetation is characterized by broom-sedge *(Andropogon virginicus)* and numerous other smaller species such as *Aristida dichotoma, Aster ericoides, Diodella teres, Plantago aristata, Lespedeza striata,* and *Juncus tenuis.* Broom-sedge is easily the dominant plant in this community (Figure 1) and grows in clumps uniformly distributed over the area. Most of the other species grow in the spaces between the clumps or in small open areas not yet occupied by broom-sedge. As pine comes in, this herbaceous

TABLE 7. DENSITY (D) AND FREQUENCY (F) OF SHRUBS AND WOODY VINES

Species		Stand Age 9	13	21	31	56	83	110
**Bignonia radicans*	d	4.6	17.3	..		39.9	.1	.7
	f	20	30	.		90	10	30
Parthenocissus quinquefolia	d	.4	1.1	.	4 6	8 0	3.2	19.6
	f	20	20		90	80	90	80
Rubus cuneifolius	d	1.5	..					..
	f	10	.			..	.	
Rubus flagellaris	d	.1		.4	.3	.3		
	f	10	..	30	20	20		
Polycodium neglectum	d	..	.1	.2	. .	2 7	.4	10.6
	f	..	10	20		70	20	90
Toxicodendron toxicodendron	d		1	2 0		3 3	4	.3
	f	.	10	50		50	10	20
Ascyrum hypericoides	d	. .		.1				
	f	..		10	.			
Benzoin aestivale	d	.		1 7	.	4.1		.
	f	. . .		40		70		.
Smilax bona-nox	d		.	.1	.			4
	f	.		10	.			10
Smilax glauca	d	.	.	9	.6	.1	.9	.9
	f	.		20	20	10	50	30
Smilax rotundifolia	d	..		1	.		.3	3.3
	f	....		10			30	70
Cyanococcus vacillans	d	.	.	.1	.	.		
	f			10				
Viburnum rafinesquianum	d	. .		4.3	1.6	4.9	5.8	2.1
	f	. .		100	60	70	90	70
Muscadinia rotundifolia	d	...	.	.1	.7	.7	4.8	8.5
	f	.		10	20	20	60	30
Celastrus scandens	d		.	.	1			
	f	..			10			
Nintooa japonica	d	.	.		2 9	5		.
	f	.			20	10		
Rosa virginiana	d	.	.	..	1 6		.	
	f	..		...	10	.		
Ceanothus americana	d	...	...	..	...	1 1		
	f	....	..	...	..	10		
Evonymus obovatus	d		.		.	.4	.9	...
	f	.	.	. .	.	10	10	
Ilex decidua	d	.	.	..	.	.1	.	
	f	.		.	. .	10	.	
Phenianthus sempervirens	d	.	.	..	.	3.2	.9	1 8
	f	.	. .	. ..	.	40	10	20
Rhus copallinum	d	.	. .	..	..	.1	.	.1
	f	...	. ..	.	. .	10	.	10
Vitis aestivalis	d	..	.	.	....	.4	.5	7
	f	. .		.	..	20	30	50
Viburnum acerifolium	d	..	. .	. .	. .	.	.8	
	f	....	. .		. .	. .	10	.
Cyanococcus corymbosus	d	...	. .	.. .	.. .	. ..	....	1 7
	f	....	.	...	...	...	....	10

*In the old field Bignonia had a density of 33.6 based on a 4-milacre quadrat and a frequency index of 90.

vegetation falls off sharply in number of species and abundance of individuals and other species gradually replace those which disappear. In the middle-age classes of pine, the herbaceous flora is very sparse. This barren condition of the forest floor may be noted in Figure 3. Nevertheless, there are certain

TABLE 8. DENSITY (D) AND FREQUENCY (F) OF HERBS

Species		Old field	Stand Age 9	13	21	31	56	83	110
Acetosella acetosella	d	6	4 9						
	f	20	20						
Agrostis alba	d	.25	.8		.2	1			
	f	20	40		20	10			
Andropogon ternarius	d	.2							
	f	20							
Andropogon virginicus	d	13.65	.3	6 8		2 1			
	f	100	30	50		60			
Aristida dichotoma	d	7 85							
	f	30							
Aster dumosus	d	05							
	f	05							
Aster ericoides	d	2 65	2	4	8	1 7			2
	f	100	10	30	20	40			10
Chamaecrista fasciculata	d	75	3	3 6	2 1	.1	1		
	f	50	30	80	90	10	10		
Cyperus sp.	d	.45							
	f	40							
Diodella teres	d	6 4	5	3.5		1			
	f	80	30	60		10			
Erigeron ramosus	d	15							
	f	10							
Gnaphalium obtusifolium	d	2	2	5		.3			
	f	20	20	40		10			
Gnaphalium purpureum	d	.5	8	1 3					
	f	40	40	60					
Gymnopogon ambiguus	d	3	2	1 8	2 7				
	f	30	20	50	60				
Helenium tenuifolium	d	1							
	f	10							
Juncus tenuis	d	3 55	2	1		1			
	f	60	10	10		10			
Kneiffia fruticosa	d	.05	1	1					
	f	05	10	10					
Lechea tenuifolia	d	05							
	f	05							
Lespedeza striata	d	4 95		2 3					
	f	80		10					
Plantago aristata	d	8 65							
	f	70							
Polypremum procumbens	d	.25							
	f	20							
Potentilla canadensis	d	.3				1 1		.3	
	f	10				50		20	
Panicum sphaerocarpon	d	3				1 7	1		.3
	f	30				50	10		10
Sarothra gentianoides	d	.35	.2						
	f	30	20						
Scirpus sp.	d	.25							
	f	10							
Solidago altissima	d	.95	7						
	f	30	20						
Solidago juncea	d	15		2.2		.4			
	f	15		40		30			
Solidago nemoralis	d	45	.1	1 2		1	1		
	f	30	10	40		10	10		
Specularia perfoliata	d	.1							
	f	10							
Strophostyles umbellata	d	.2		.1	.4				
	f	20		10	30				
Syntherisma sanguinale	d	.2							
	f	20							

TABLE 8. *(Continued)*

Species		Old field	Stand Age						
			9	13	21	31	56	83	110
Trifolium arvense	d	.3	.1	.2					
	f	30	10	20					
Ambrosia elatior	d		.2	.4	.1				
	f		10	40	10				
Asplenium platyneuron	d		.3						
	f		10						
Capriola dactylon	d		8.0	41.9					
	f		20	100					
Leucanthemum leucanthemum	d		.1						
	f		10						
Eupatorium capillifolium	d		.1						
	f		10						
Eupatorium hyssopifolium	d		.2	.2	.8	1.6	.2		
	f		20	10	20	60	20		
Falcata comosa	d		1			.6	.4	.1	
	f		10			30	30	10	
Quamoclit coccinea	d		.4	.1					
	f		10	10					
Juncus setaceus	d		3						
	f		20						
Panicum sp.	d		.1						
	f		10						
Passiflora incarnata	d		2						
	f		10						
Physalis virginiana	d		3	.7	.1				
	f		10	30	10				
Rynchosia erecta	d		.2		4	5	6		
	f		10		30	20	30		
Tragia urens	d		.1	.4					
	f		10	10					
Martiusia mariana	d			.1					
	f			10					
Eragrostis pilosa	d			3		.5			
	f			20		30			
Hieracium greenii	d			.6					
	f			20					
Lactuca sagittifolia	d			.1					
	f			10					
Meibomia arenicola	d			.6	.2				
	f			20	10				
Meibomia viridiflora	d			.9					
	f			20					
Xanthoxalis sp.	d			.3					
	f			20					
Andropogon sp.	d				.7				
	f				50				
Aster patens	d				.1		.3		
	f				10		20		
Chimaphila maculata	d				5.2	.4	2.0	.8	.2
	f				100	30	80	50	20
Crotalaria sagittalis	d				.1	.3	.1		
	f				10	30	10		
Lespedeza repens	d				1.0	.1			
	f				20	10			
Panicum ravenelii	d				.2				
	f				10				
Polygonatum biflorum	d				.1			.1	.1
	f				10			10	10
Biventraria variegata	d					.6			
	f					50			
Carex sp.	d					.1			
	f					10			

TABLE 8. *(Continued)*

Species		Old field	Stand Age						
			9	13	21	31	56	83	110
Elephantopus tomentosus	d					.5	5	2 4	2.2
	f					20	20	20	40
Aristolochia serpentaria	d						.2	.2	.3
	f						10	10	10
Cracca spicata	d						2		
	f						10		
Galium sp.	d						.2	.1	.3
	f						20	10	30
Meibomia marylandica	d						1		.7
	f						10		20
Ruellia ciliosa	d						2		
	f						10		
Solidago boottii	d						1		
	f						10		
Sorghastrum nutans	d						1	1	
	f						10	10	
Peramium pubescens	d							7	
	f							20	
Tithymalopsis corollata	d							.5	4
	f							30	30
Panicum boscii	d							.1	
	f							10	
Hexastylis virginica	d								.4
	f								10
Botrychium obliquum	d								.1
	f								10
Geum canadense	d								.1
	f								10
Gnaphalium sp.	d								.1
	f								10
Grass	d								1.0
	f								10
Potentilla pumila	d								1
	f								10
Viola sp.	d								.7
	f								20

species which are typical of these age classes. These include *Chimaphila maculata, Eupatorium hyssopifolium,* and *Rynchosia erecta.* Slowly, the characteristic herbs of the mature stand become more numerous and species such as *Elephantopus tomentosus, Aristolochia serpentaria, Polygonatum biflorum, Tithymalopsis corollata,* and *Hexastylis virginica* become apparent. To what extent this flora continues on into the hardwood community is not known, but it is definite that some of the herbs such as Hexastylis and Polygonatum are found in some abundance in mature oak-hickory stands.

As a rough measure of the trend of homogeneity of the vegetation during succession, frequency graphs were employed. The frequency data were grouped into five classes as follows (Raunkiaer, 1918) : Class A, those species appearing in from 1 to 20 percent of the quadrats of a given size in any one stand; Class B, those species appearing in from 21 to 40 percent of the quad-

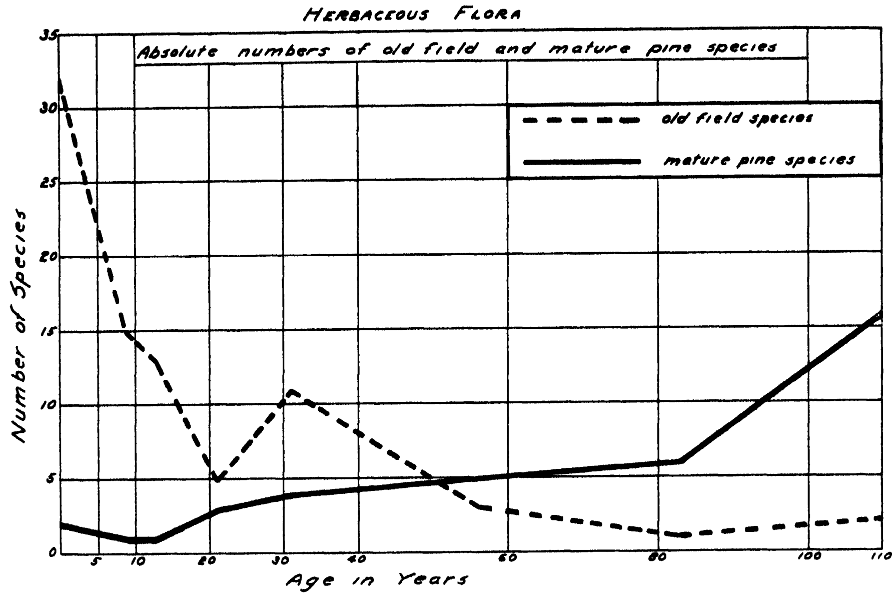

Fig. 8. The total number of old field herbaceous species throughout the succession contrasted with the total numbers of those herbaceous species which are present in the mature pine stand.

rats; Class C, those species appearing in from 41 to 60 percent of the quadrats; Class D, those species appearing in from 61 to 80 percent of the quadrats; and Class E, those species appearing in from 81 to 100 percent of the quadrats. Raunkiaer (1918), in summing up frequencies of over 8,000 examples, found that the species were distributed through the five classes as follows: Class A, 53 percent; Class B, 14 percent; Class C, 9 percent; Class D, 8 percent; and Class E, 16 percent. These percentages, when plotted, form a normal fishhook or J-shaped curve. According to Raunkiaer's "Law of Frequence", this curve results when analyzing the data from an association in a state of relative equilibrium. At this point, one or several species prosper at the expense of their neighbors and constitute the species to be found in the highest frequency classes. At the other end of the scale, many occasional and accidental species fill up Class A. The result, then, is a curve with a peak in Class A and another lower peak in Class E.

Series of graphs were constructed for each size of quadrat employed and also for the vegetation as a whole using the data from the different quadrat sizes. This latter would not ordinarily be possible since reliable graphs cannot be constructed from data obtained from quadrats which are not of a uniform size. However, in this case, different synusiae of the same association were sampled separately on special quadrat sizes so that no error is introduced and in combining the frequency data from the different synusiae a fair idea of the homogeneity of the vegetation of the entire phytocoenosis can be obtained.

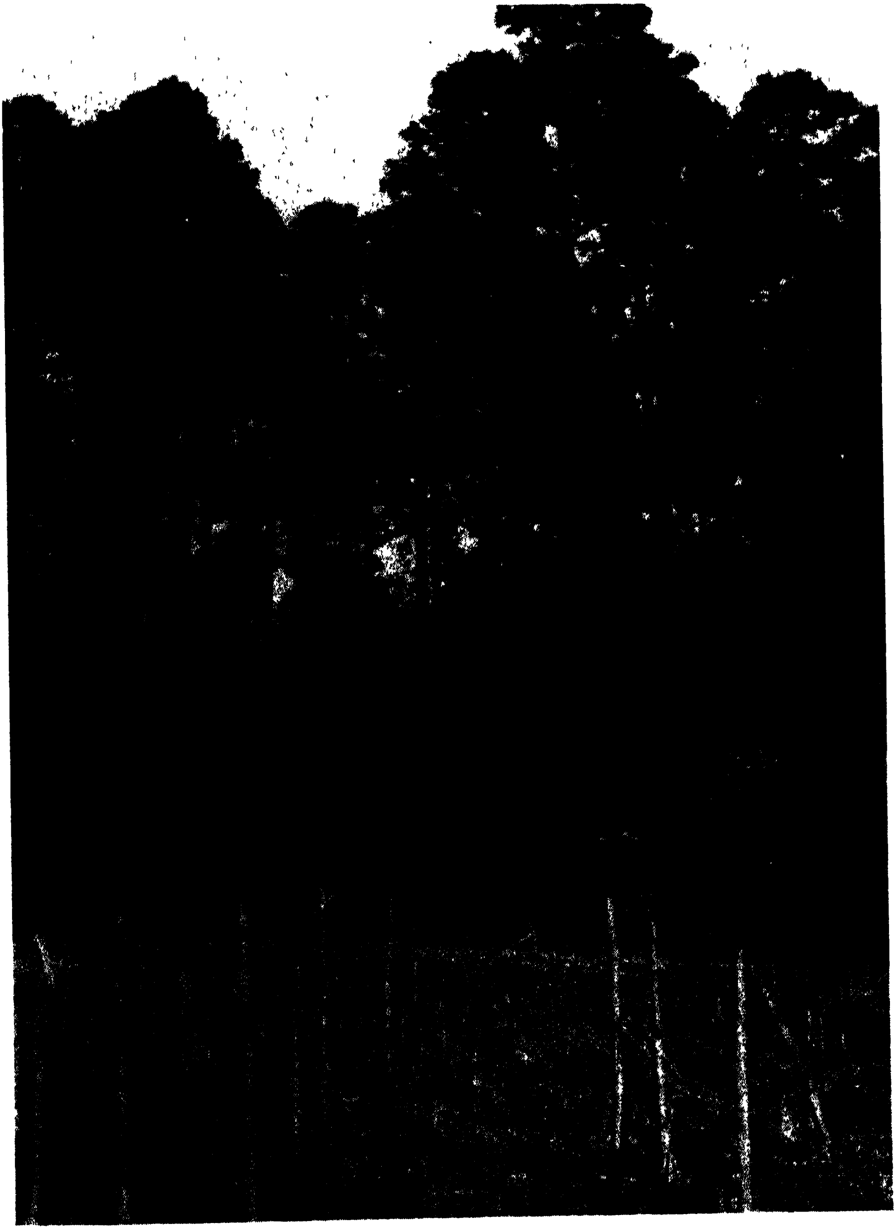

FIG. 9. Stratification as illustrated in an 85-year old shortleaf pine stand. The secondary arborescent stratum is made up of *Cornus florida* (blooming), *Quercus*, and other hardwoods.

In Figure 10, the graphs for the ¼-milacre quadrats showing frequency indices of herbs are arranged in successional order. The striking fact exhibited by these curves is that, in the old field, the herbs form a fairly

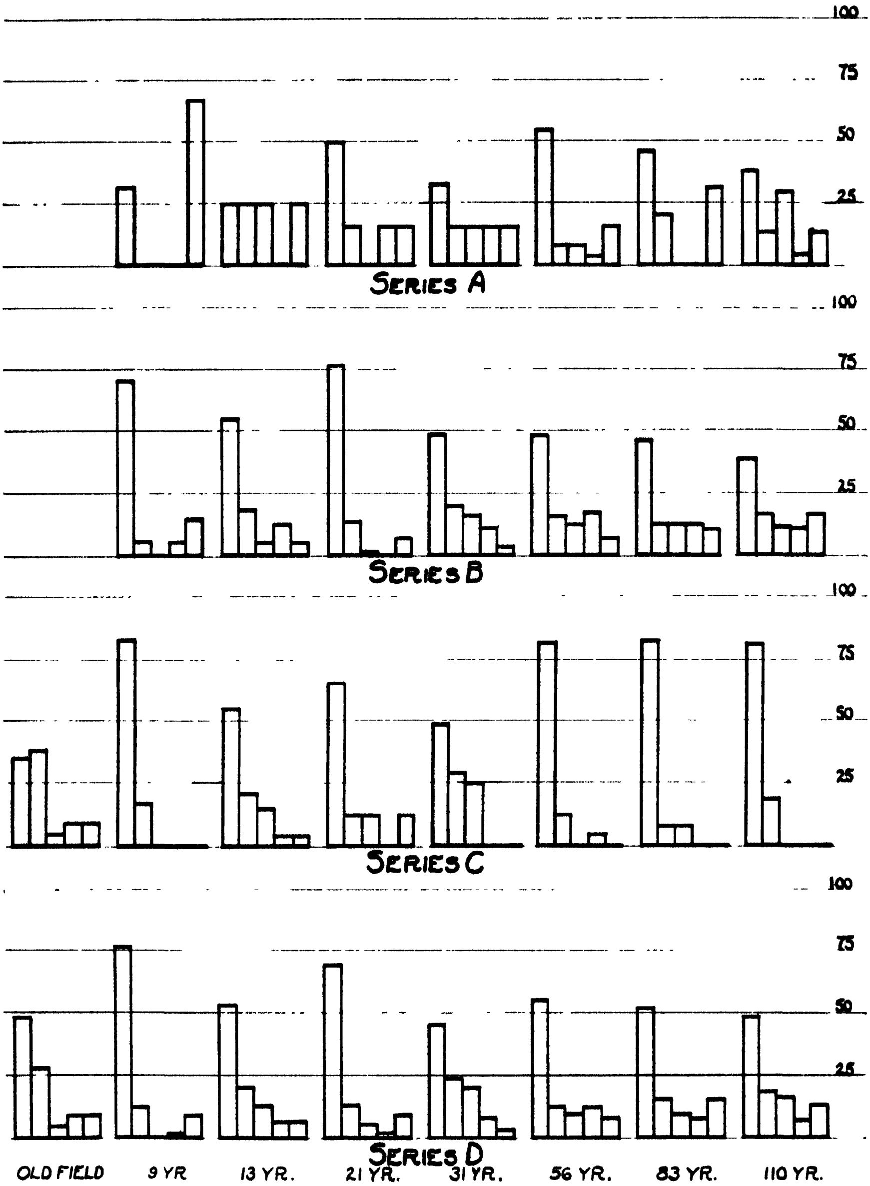

FIG. 10. The trend of the frequency curve through the succession as exhibited by the curves for the arborescent strata, the shrubby layer, the herbaceous layer, and the vegetation as a whole.

homogeneous community but as succession progresses, they become more and more scattered and less uniformly distributed throughout the association. This is indicated by the tendency of over 80 percent of the species to occur in the lowest frequency class in the oldest pine stands while few or none occur in the highest frequency classes in the same stands. Thus, the curves are very high in Class A and disappear entirely in Class E.

The vegetation of the shrubby layer shows a decided trend toward greater homogeneity as a stand approaches maturity. As is illustrated in Figure 10, the species of this stratum are at first mostly scattered throughout the stand but gradually become more evenly distributed and the result is a decrease in height of the peak in Class A and marked increases in the higher frequency classes. This same trend, though less pronounced, is followed by the species in the arborescent strata.

The lower series of curves in Figure 10 considers the vegetation as a whole. The abandoned field with its herbaceous vegetation is in a fairly homogeneous condition but this is considerably disturbed by the entrance of the pines as the frequency curve for the 9-year stand shows an unusually high peak in Class A, no species at all in Class C, and a low peak in Class E. As succession progresses, the vegetation becomes more homogeneous and the frequency curves for the oldest stands come remarkably close to Raunkiaer's normal denoting a close approach to a state of relative equilibrium.

RESULTS OF SOIL INVESTIGATIONS

COMPARABILITY OF THE STATIONS

THE PROFILE

The field data on the soil profile and also that on mechanical analysis show the succession to be worked out on inherently comparable light-textured lower Piedmont soils. The soil profile is characterized by a relatively thick (14 to 28 inches) A horizon of sandy loam underlain by a narrow (10 inches) B_1 horizon containing somewhat more clay and a relatively heavy B_2 horizon averaging about 15 inches in thickness. The almost unweathered C horizon extends to at least 8 feet in some instances.

The observed changes in the profile seem to be limited to the first few inches, so that a general description of the various horizons will suffice for all the stands. The A_2 horizon is a yellowish sandy loam of single grain structure which averages between 9 and 17 inches in thickness. The relatively narrow B_1 horizon is a friable, dull yellow sandy loam or sandy clay loam which is characterized by the presence of numerous black concretions about ¼-inch in diameter. This peculiarity of the B_1 horizon is found in every stand. The B_2 horizon is a compact, bright yellowish red sandy clay or clay. The C horizon underlying the B_2 horizon is a friable sandy clay or sandy clay loam. It is usually grayish in color, marked with splashes of red.

MECHANICAL ANALYSIS

In order to show that the soils in all the stands are similar in texture, the data from the mechanical analysis of one profile selected at random in each stand are given in Tables 9 to 14. Table 9, presenting the values for the surface of the mineral soil, shows that, in all the stands, the total sand content for this part of the profile is around 80 percent. The amount of clay ranges between 5 and 7.5 percent and tends to increase slightly in the older stands. This increase is undoubtedly due, for the most part, to the addition of organic colloids and not to any outstanding irregularities in the mineral soil, since the organic matter was not oxidized before mechanical analysis. According to the classification of Davis and Bennett (1927), the two oldest stands have a surface soil which is a sandy loam while all the other stands are on loamy sands. However, in all cases, the values for sands and clays come very close to the borderline between these textural grades. As far as the mineral soil is concerned, all the stands seem to be comparable.

In the younger stands, a cultural or "plowed" horizon was observed which had resulted from the mixing together of the surface soil during cultivation. This "plowed" horizon (Table 10) is very similar to the soil at the surface, being of the same textural grade. It has a sand content of from 80 to 82 percent and approximately 7 to 9 percent clay. With the exception of that in the 56-year stand, the A_2 horizons are all sandy loams ranging from approximately 73 percent to 78 percent sand content and from 9 to 14 percent clay content. The A_2 under the 56-year stand is a loamy sand with 82 percent sand and 7 percent clay. The mechanical analysis data for the A_2 horizon appear in Table 11.

The texture of the B_1 horizon is more variable. However, in all but two cases it is a sandy loam. These exceptions are a B_1 of sandy clay loam in the 9-year stand and a sandy clay B_1 in the 31-year stand. The percentages of the various size fractions in this horizon are included in Table 12.

The horizon having the greatest percentage of clay is the B_2. It is the most variable of the horizons, ranging from a sandy clay loam to a clay. It has its heaviest texture in the 31- and 110-year stands and is lightest in the old field. Table 13 shows the variation for this horizon among the stands.

The C horizon is more sandy than the B_2 and ranges from a sandy loam to a sandy clay. This horizon frequently contains veins of practically pure clay which are sometimes found as deep as 8 feet. Table 14 shows the percentage for the size classes in the C horizon.

From these data, it can be seen that the soil is sandy throughout the whole profile; yet it contains enough clay to provide a medium for base exchange and also enough to prevent excessive percolation of water. The texture of the upper three horizons in all the stands is very much alike. The texture of th B_2 horizon varies somewhat but scarcely enough to influence plant growth to any great extent, especially since only a very few roots extend as deeply

TABLE 9. MECHANICAL ANALYSIS* OF SURFACE SOIL

Age of stand	Total sands	Total "colloids"	Silt	Clay	Fine clay
Old field	83 59	9 38	10 54	5 87	4 37
9 years	81 77	8 21	13.03	5.20	4.20
13 years	83 07	8 57	11 37	5 56	3 92
21 years	82.41	9 07	11 52	6 07	4.56
31 years	80 01	9 95	13 05	6 94	4.93
56 years	81 64	8 31	12 06	6 30	4 80
83 years	76.67	11 26	16 09	7 24	5 22
110 years	78 27	11 69	14 06	7 67	5 66

*The mechanical analyses are expressed in percentage.

TABLE 10. MECHANICAL ANALYSIS OF "PLOWED" HORIZON

Age of stand	Total sands	Total "colloids"	Silt	Clay	Fine clay
Old field	79 93	13 04	11 04	9 03	6 88
9 years	81 77	10 21	11 52	6 71	5 71
13 years	81 06	9 57	12 02	6 92	4 92
21 years	81 42	11.57	10 01	8 57	7 57

TABLE 11. MECHANICAL ANALYSIS OF A_2 HORIZON

Age of stand	Total sands	Total "colloids"	Silt	Clay	Fine clay
Old field	73 57	15 40	16 04	10 39	8 38
9 years	75 38	15 60	13 89	10 73	8 22
13 years	78 06	13 93	12 52	9 42	6 92
21 years	72 74	18.24	12 67	14 59	12 59
31 years	77 01	17 62	11 03	11 96	9 95
56 years	82 06	9 93	10 66	7 28	5 92
83 years	74 14	14 85	16 01	9 85	8 20
110 years	78 34	13 65	13 02	8 64	7.64

TABLE 12. MECHANICAL ANALYSIS OF B_1 HORIZON

Age of stand	Total sands	Total "colloids"	Silt	Clay	Fine clay
Old field	76 90	16.07	11 05	12 05	10 04
9 years	66 25	26 71	12 07	21 68	19 31
13 years	67 86	23 07	13 09	19 05	17 03
21 years	70.69	21 28	12 05	17 26	16 62
31 years	54 50	34 36	15 19	30 31	28 28
56 years	71 23	20 73	11 92	16 85	15 35
83 years	67 01	23 95	13 70	19 29	17 28
110 years	68 20	22 75	13 07	18 75	16 72

TABLE 13. MECHANICAL ANALYSIS OF B_2 HORIZON

Age of stand	Total sands	Total "colloids"	Silt	Clay	Fine clay
Old field	69.20	23.70	10 14	20 66	18 63
9 years	50 66	43.24	10 16	39 18	36 78
13 years	59.19	33 72	10 13	30 68	27.64
21 years	56 40	35 52	12 12	31 48	30 48
31 years	31.41	53 87	21 53	47 06	42 96
56 years	57.06	36 84	10 16	32.78	31.77
83 years	60 92	29.24	13.83	25 55	23.52
110 years	49.36	43.50	11 22	39 42	37.38

TABLE 14. MECHANICAL ANALYSIS OF C HORIZON

Age of stand	Total sands	Total "colloids"	Silt	Clay	Fine clay
Old field*	....	..	...	.	
9 years	65.04	25.85	14.16	20.80	19.78
13 years	63.21	23.61	16.59	20.20	18.54
21 years	53.32	37.59	13.13	33.55	31.53
31 years	55.08	28.66	23.01	21.91	20.24
56 years	67.90	27.02	8.49	23.61	21.59
83 years	63.40	24.47	17.19	19.41	17.39
110 years	49.18	41.60	13.31	37.51	35.46

*No samples collected because of abnormal height of water-table at time of collection.

as this horizon. The one effect of the heavier B horizons would be in slowing down percolation so that these stands would remain moist for a longer time in the spring. During the growing season, however, such a heavy B_2 horizon would have very little effect on the moisture relations of plant and soil, since the summer rains seldom penetrate deeper than a few inches.

CHANGES

EVOLUTION OF THE PROFILE

That there is a distinct change in the upper part of the soil profile, is evident from Figure 11. This figure shows the development of the soil profile during its 110-year occupancy by the pine, plotted from the average thicknesses of the mineral and organic horizons in each stand.

In the abandoned field, there is, at the top of the mineral profile, a layer, almost 12 inches thick, which is dark yellowish brown in color. This layer or horizon is very homogeneous and is the visible effect of cultivation. Hence, it will be referred to as the "plowed" horizon. The organic horizons are practically absent in the old field, there being only a very little herbaceous litter.

In the 9- and 13-year old pine stands, the "plowed" horizon is thinner than that in the old field, being little over 6 inches thick. In these same stands, there is a marked increase in the thickness of the litter and the appearance of a fermentation layer of partially decayed needles.

Progressing to the 21-year age class, it is seen that the *brown* "plowed" horizon is overlain with a very thin (0.5 inch) *blackish gray* A_1 horizon. The "plowed" layer has gradually become thinner and the distinctly different colored A_1 horizon develops over it and eventually replaces it. The total thickness of the organic horizons in this stand is about 1½ inches. The humus layer is still absent.

In the 31-year stand, the "plowed" horizon has completely disappeared and the blackish gray A_1 horizon has become almost 3 inches thick. The total thickness of the organic horizons in this stand is not as great as that in the 21-year stand but it is marked by the first appearance of a humus layer, in addition to the litter and fermentation layers.

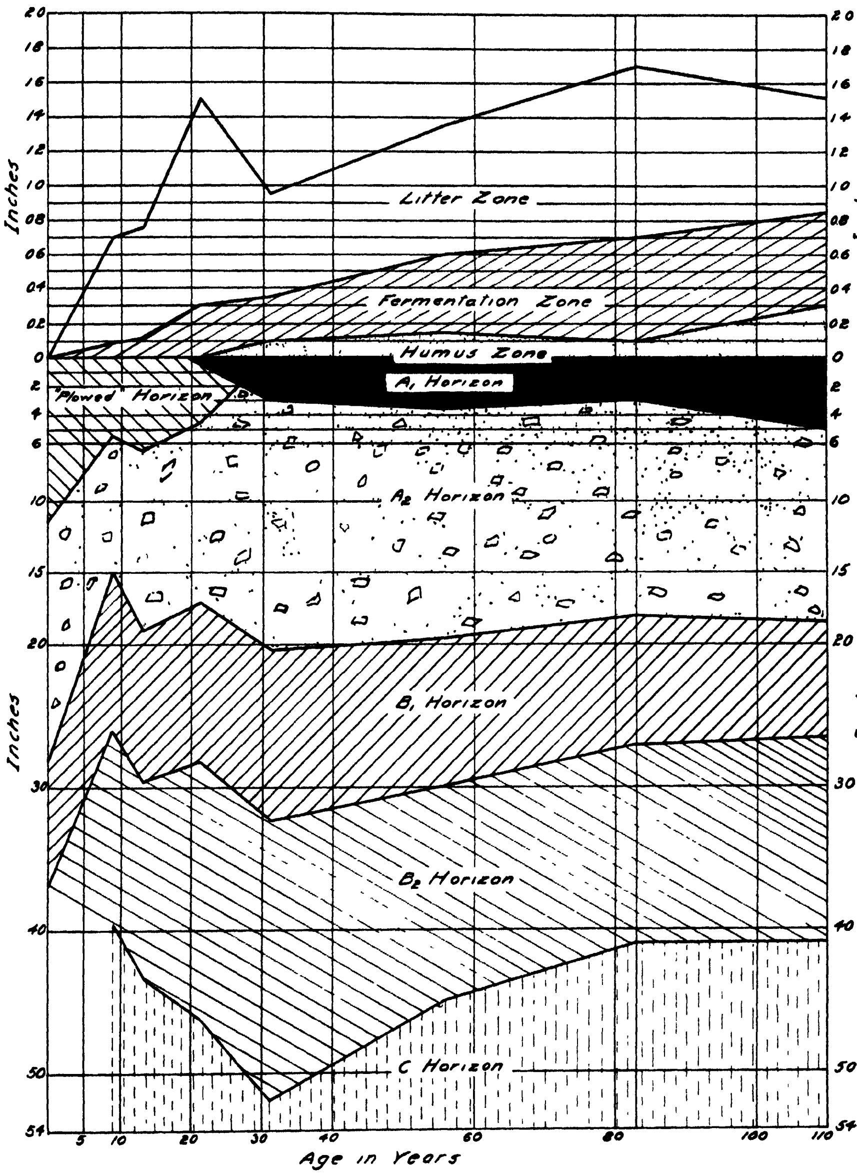

FIG. 11. Profile development under pure stands of shortleaf pine. Note the increase in depth of the organic horizons and the gradual replacement of the "plowed" horizon by the A_1 horizon.

From the 31-year stand to the 110-year stand, the general trend of the profile development is toward a thicker A_1 horizon which gradually acquires a good crumb structure through the addition of organic matter and the activity of soil fauna. The organic horizons tend to increase in total thickness,

seldom, however, becoming much over 1½ inches deep. Both the fermentation and the humus layers show marked increases in thickness but the litter remains more nearly constant. The profile under the pine, then, has the appearance of a podsolic soil with some organic accumulation on the surface, a dark A_1 horizon, a bleached or light-colored A_2 horizon, and a zone of accumulation in the B horizons.

ORGANIC MATTER

The results obtained by the wet combustion method for the determination of organic matter are presented in Table 15. These results for the surface

TABLE 15. AVERAGE ORGANIC MATTER CONTENTS BY THE WET COMBUSTION METHOD (Percentage of oven-dry weight)

Stand	Surface	"Plowed"	A_2	B_1
Old field	C 852	0.706	0 190	0.193
9 years	0.823	0 487	0.198	0 175
13 years	0 707	0 437	0 147	0 070
21 years	1.328	0.684	0 328	0 331
31 years	1.649		0 451	0 2206
56 years	1.792		0 275	0.179
83 years	2.795	.	0.371	0 206
110 years	2.944	.	0 474	0 215

soil and the A_2 horizon are shown graphically in Figure 12 as are also the values for the same horizons obtained by the ignition method. The surface soil shows a marked trend toward increased organic matter content with increased age of stand. The surface soil of the abandoned field and the younger stands shows less than 1 percent organic matter by the wet combustion method while that of the mature pine stand shows almost 3 percent organic

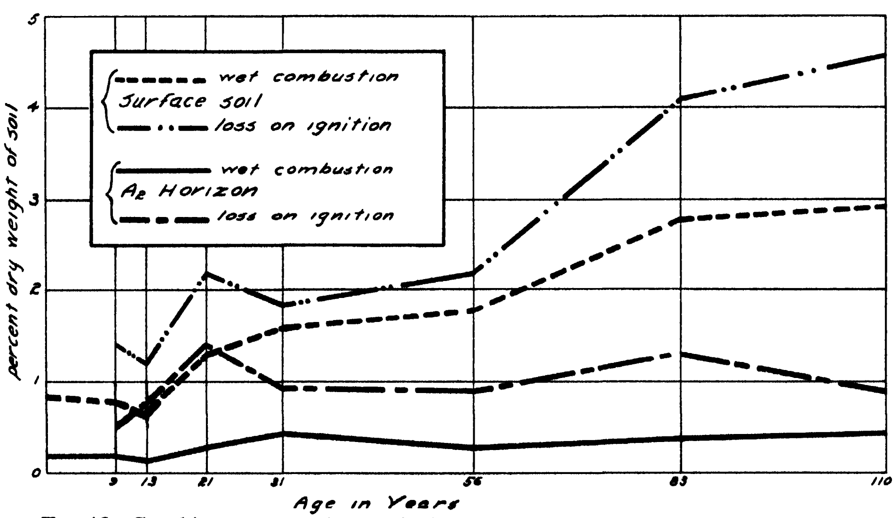

FIG. 12. Graphic representation of the increase in organic matter throughout the shortleaf pine succession.

matter by the same method. The amount of organic matter is low in the A_2 and is still lower in the B_1. There is a slight tendency toward increase in organic matter with age in both these horizons. The values obtained from loss on ignition run higher in every case than those obtained by the wet combustion method due to the driving off of the bound water and the water of hydration in the colloids.

MOISTURE EQUIVALENT

The data shown in Table 16 are the average moisture equivalents for the different horizons through the pine succession. Since the moisture equivalent is a function of the amount of colloidal material in the soil, it would be expected to increase with an increase in colloidal content. Although the texture of the surface soil is essentially the same in all stands of the successional series, the moisture equivalent increases due to the previously mentioned in-

TABLE 16. AVERAGE MOISTURE EQUIVALENTS

Stand	Surface	"Plowed"	A_2	B_1	B_2	C
Old field	6 84	8 32	8 14	10 015	17 17	.
9 years	6 45	6 67	7 40	15 07	28 00	20.12
13 years	6 06	6 22	7 31	13 29	20 30	20 18
21 years	7 20	6 80	9 71	13 29	22 21	25 31
31 years	7 685		8 24	17 26	28.70	24 03
56 years	7.33		7 08	14 49	28 14	17 89
83 years	11 52		9 31	13 81	20 75	20 18
110 years	10 43		7 29	14 92	26 87	25.54

creases in the amount of organic matter. This is substantiated by the highly significant correlation coefficient of 0.949 obtained between organic matter content and moisture equivalent of the surface soil through this succession.

In the younger stands, the surface soil has a lower moisture equivalent than the A_2 horizon because of the former's inherently lower content of inorganic colloids. However, in the older stands, the moisture equivalent of the surface soil is higher than that of the A_2 horizon. The surface soil in the older stands is still below the A_2 in total "colloidal" content as determined by a hydrometer, but it has a higher moisture equivalent because of the addition of organic colloids which are much more hygroscopic than inorganic colloids. As would be expected, the horizons having the greater amounts of clay have the higher moisture equivalents. The B_2 horizon, in general, shows the highest values of the profile, these values ranging between 20 and 29 percent. These results show that the only change in moisture equivalent during pine succession is an increase in the A_1 horizon due to the increase in the amount of organic colloids in that horizon.

VOLUME-WEIGHT

The volume-weight or apparent specific density of soils is a measure of compactness. These results are presented in the form of averages in Table 17.

TABLE 17. AVERAGE VOLUME-WEIGHTS

Stand	Surface	A_2	B_1
Old field	1.346	1.749	.
9 years	1.329	1.541	1.915
13 years	1 346	1 558	1.687
21 years	1 265	1 508	1.624
31 years	1.210	1.653	1 606
56 years	1 123	1.561	1.787
83 years	1.143	1 556	1 834
110 years	1 029	1.520	1 756

The surface soil is shown to be relatively porous as compared to the rest of the profile and that compactness increases with depth, at least to a certain point. There is a marked decrease in the volume-weight of the surface soil through succession from a value of 1.346 in the abandoned field to 1.029 in the mature pine stand. This same trend is shown to a lesser degree in the A_2 horizon. A highly significant correlation coefficient of —0.911 between organic matter and volume-weight in the surface soil shows that the volume-weight of the A_1 horizon is strongly associated with the organic matter content of that horizon. An increase in the amount of organic matter is accompanied by a decrease in the volume-weight. This increased porosity and lighter weight of the surface soil through succession might therefore be said to be due to increased organic matter and its attendant phenomena, presence of root channels, activities of soil fauna, and crumb structure.

TABLE 18. AVERAGE WATER-HOLDING CAPACITIES

Stand	Surface	A_2	B_1
Old field	33.705	27 084	
9 years	36 177	30 662	25 496
13 years	36 038	30 775	33 222
21 years	42 400	37 206	33 500
31 years	40 469	27.761	33 790
56 years	41.482	28 360	28 440
83 years	43 485	30.077	26 273
110 years	45.274	31 731	30 968

TABLE 19. AVERAGE AIR CAPACITIES

Stand	Surface	A_2	B_1
Old field	7.733	4.122	.
9 years	7.607	7.538	4.943
13 years	7 899	6 399	6.553
21 years	6.094	4.940	4 386
31 years	9.093	5.038	5.706
56 years	12.738	5 210	4.050
83 years	8.135	4.606	2.883
110 years	8.363	5.705	3.663

WATER-HOLDING CAPACITY

The ability of the soil mass to hold water against the pull of gravity is known as the water-holding capacity (the "Wasserkapazitat" of the German and Swiss workers). It is here expressed on a volume basis as the amount of water held per unit volume. The averages of the water-holding capacity determinations are recorded in Table 18. The averages show that to a certain point, at least, the water-holding capacity decreases with depth. Of the three horizons sampled, the surface soil, in general, has much higher values than the A_2 and B_1 horizons. No water-holding capacity determinations were made for the B_2 horizon but such determinations would probably show higher values because of the higher clay content. The only marked tendency to change under the influence of pine is exhibited by the surface soil which shows an increase from a value of 33.705 percent volume in the abandoned field to a value of 45.274 percent volume in the mature stand. This increase is due almost entirely to the addition of organic matter as is brought out by the highly significant correlation coefficient of 0.884 obtained between these two factors in the surface soil through succession. A high correlation of 0.930 was also obtained between average total thickness of the organic horizons and the water-holding capacity of the A_1 horizon. The highly significant inverse correlation of —0.840 between water-holding capacity and volume-weight in the same horizon shows the dependency of the two on the factor of organic matter and to some extent on each other.

AIR CAPACITY

The data on air capacity show no definite trend toward an increase or a decrease in this factor throughout the pine succession. Aichinger and Siegrist (1930) have shown that there is an increase in the air capacity during an alder succession on the sandy soils in central Europe. Since there is no consistent increase in this instance, it may be that more samples taken in the older stands would yield better results. As would be expected, the surface soil has the greatest air capacity ranging from 8.094 percent by volume in the 21-year stand to 12.738 percent by volume in the 56-year stand. The data, in the form of averages, are presented in Table 19.

RESULTS OF ROOT STUDIES

It is very evident from Table 20 that there is scarcely any change in the total number of roots in the whole profile after the pines have become estab-

TABLE 20. AVERAGE NUMBER OF ROOTS PER 12 SQUARE FEET OF PROFILE IN EACH STAND

Old field	114
9-year stand	262.2
13-year stand	285.6
21-year stand	276 5
31-year stand	224 75
56-year stand	247.
83-year stand	220
110-year stand	3C7.5

lished. With the closing of the crown canopy, there seems also to be a closing of the root network. During the pine dominance, at least, this network seems to be fairly constant in the total number of roots of which it is composed.

Probably the most striking feature brought out by the root studies is the fact that in all the stands most of the roots are in the upper 6 inches of mineral soil. Table 21 shows the percentage of the total roots in the profile

TABLE 21. DISTRIBUTION OF TOTAL ROOTS IN SUCCESSIVE 6-INCH DEPTHS (Percentages)

Age of stand	1st 6 in.	2nd 6 in.	3rd 6 in.	4th 6 in.	5th 6 in	6th 6 in.
Old field	95.61	4.39				
9 years	62.45	21.83	7.81	4.48	2 66	1.76
13 years	61.83	24 85	6 16	4.20	1.61	1 15
21 years	55 78	19.89	15 91	4.70	2 44	1 26
31 years	62 82	16 57	9 34	4 56	5 22	1.44
56 years	60.82	21 25	9 41	4 35	2 93	1 21
83 years	63 18	17.27	11.36	4 36	2.86	.90
110 years	64 14	16 82	7 80	2 60	4 71	3 90

which are found in successive 6-inch depths. In the abandoned field, populated with shallow-rooted herbs, over 95 percent of the roots are in the first 6 inches and the remainder are in the second 6 inches. With the entrance of the pines and other woody species, deeper pentrating roots appear and the percentage of total roots of the profile in the first 6 inches falls to a little over 60 percent. Here again an equilibrium seems to be established with the closing of the crown canopy since there are no significant changes in the concentration of roots in the different depths until the stand is mature. In the mature pine stand, there is a slightly higher number of roots at the deeper depths. This may be a result of the better utilization of the soil by the deeper rooted species which enter late in the pine stage. Again, it may be the result of the slightly higher colloidal content in the lower part of the 3-foot section in the oldest stand.

Since most of the roots are in the upper 6 inches of soil, it would be expected that the soil horizons in that zone would contain higher percentages of the total roots than would the deeper horizons. This is shown to be the case in Table 22. The "plowed" horizon up through the 21-year old stand con-

TABLE 22. DISTRIBUTION OF TOTAL ROOTS THROUGH THE VARIOUS HORIZONS (Percentages)

Stand	A_1	P_L	A_2	B_1	B_2	C
Old field	.....	98.24	1.76	...	....	...
9 years	. ..	59.84	27.65	6.19	5.72	.57
13 years	....	70.58	22.96	4.65	1.75	. .
21 years	2.16	47.19	43.12	6.05	1.44	....
31 years	34.48	.....	55.28	8.12	2.11	....
56 years	42.20	.....	48.98	6.57	2.22	....
83 years	37.72	.....	53.77	6.36	2.09	....
110 years	60.73	.....	26.66	4.79	7.80	....

tains the greater part of the roots of the profile. The A_1 horizon, as it grows thicker, contains an increasing percentage of the total roots. It is only in the oldest pine stand, though, that it contains more roots than the A_2 horizon. However, the A_1 horizon is always thinner than the A_2 and contains more roots per unit area of profile exposed than does the latter. Tamm (1920), in Sweden, found that roots tended to avoid the light-colored A_2 horizon. In the stands considered in the present study, however, this is not the case. They are not as abundant per unit area in the A_2 horizon but there seems to be no indication of an avoidance of this area by roots. This conforms with the findings of Hesselman (1910) in northern Sweden and Laitakari (1929) in Finland, both of whom worked with Scotch pine *(Pinus sylvestris)* on sandy soils. In all the stands in the present study, less than 13 percent of the total roots occurred in the B horizons.

The percentages of the various size classes of roots in each stand are presented in Table 23. In all but one stand, over 80 percent of the roots range

TABLE 23. DISTRIBUTION OF TOTAL ROOTS IN THE VARIOUS SIZE CLASSES (Percentages)

Stand	0.01-0.1 in	0.11-0.3 in.	0.31-0.5 in.	0.51-1 in.	Over 1 in
Old field	100				
9 years	92.75	5.91	1.14	0.19	
13 years	86.48	11.55	1.15	0.70	.10
21 years	86.16	10.84	1.89	0.99	.09
31 years	83.20	13.45	2.22	0.89	.22
56 years	85.02	10.62	1.82	1.92	.60
83 years	79.36	13.63	3.00	2.27	1.63
110 years	85.36	9.67	2.43	1.54	.97

from 0.01 to 0.1 inch in diameter. Here also there seems to be an equilibrium established with the closing of the root network. In the old field, all the roots are of this smallest size class. In the 9-year stand, the percentage of the smallest roots falls to approximately 93 percent and in the 13-year stand to approximately 86 percent, after which the percentage remains practically constant all through the pine succession. The only other change of any significance, as regards size of roots, is the increase in number of larger roots in the older stands. This, of course, is the natural result of the increase in size of the trees.

To show the locations and numbers of the various sized roots in the profiles of three representative stands, Figures 13 to 15 have been constructed from the average number of roots of each size class in successive 6-inch depths. These figures show graphically the fact that most of the roots are in the upper 6 inches of the soil. They also show that the smaller roots are relatively more numerous in the first 6 inches than they are in the second 6 inches, because of the fact that many of the larger roots are found between the 6- and 18-inch depths while the smaller roots are located closer to the

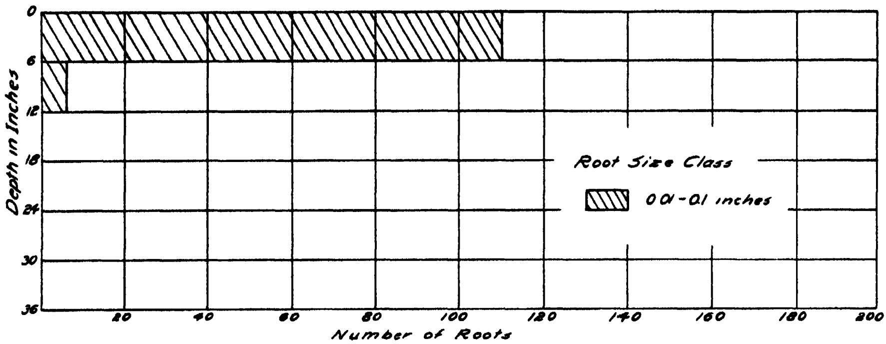

FIG. 13. Average number of roots per standard profile in the abandoned field arranged according to depth and size class.

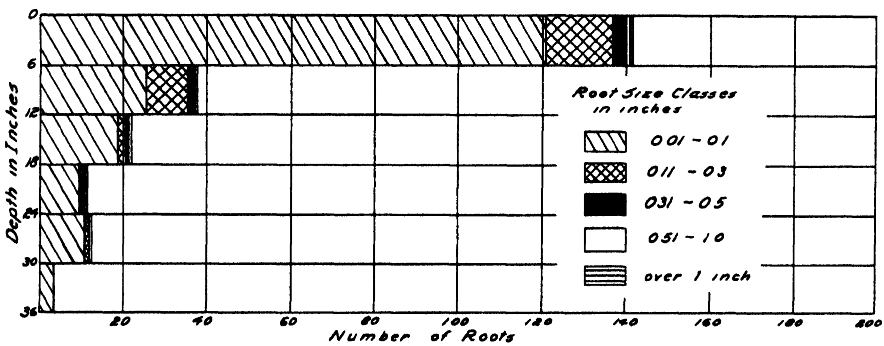

FIG. 14. Average number of roots per standard profile in the 31-year old pine stand arranged according to depth and size class.

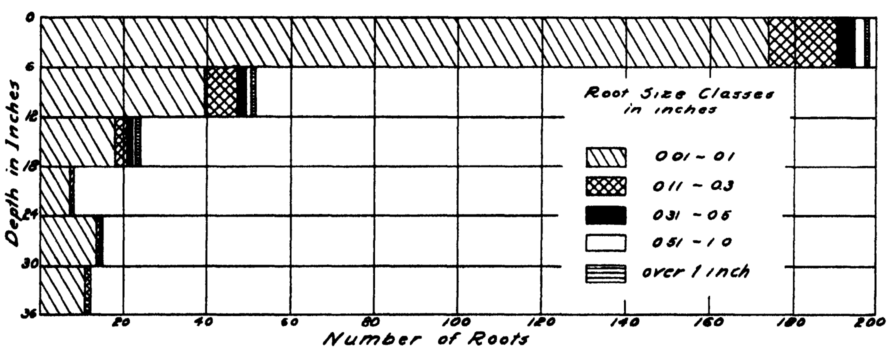

FIG. 15. Average number of roots per standard profile in the 110-year old pine stand arranged according to depth and size class.

surface. The tendency of roots to penetrate more deeply in the older stands is also apparent from the diagrams.

These same data arranged on a horizon basis are not included in tabular or graphic form. It will suffice to say that in practically every case, the "plowed" and A_1 horizons show the great numbers of the smallest size class

only and that the greatest numbers of all the larger size classes are in the A_2 horizon. Most of the roots in the B horizons are very small, although occasionally larger ones are present, especially in the older stands.

CORRELATION AND INTEGRATION

In any analysis of plant succession, many factors must be considered. The slow but constant change, both in the vegetation and the environment, cannot be completely interpreted in terms of any one factor. It is, rather, a complex of factors which is both the cause and effect of change. Because of the delicate balance between the factors of the environment, it is impossible for one factor to change without affecting others and these, in turn, may affect still others. Thus, the environmental complex itself is subject to change at the slightest stimulus and the result is far-reaching readjustments within the whole organismo-environmental system. Early in succession, the complex is especially unstable and consequently there are rapid changes as revealed by constant readjustments in the vegetation and the soil. Later, through the approaching of equilibria among some of the factors, there is a gradual retardation of change, the decrease continuing to a condition of near-stability. This state of near-stability, which is never absolute, is commonly known as the climax condition.

It has been the purpose of this study to determine certain of these changes in the vegetation and the soil during the early stages of forest succession and to attempt to evaluate and integrate them. By delimiting the work to areas essentially comparable in topography, climate, and soils, it has been possible to study the mutual effects of the vegetation and the physical properties of the soil during succession and the changes in the organismo-environmental complex produced by these mutual effects.

The virgin deciduous forests which occupied these areas of light-textured Lower Piedmont soils at the time of the coming of the white man were probably in the near-stable climax condition. They were climax not only as regards vegetation but also as to soil which was mature with well-developed horizons. Cain (1932a) has shown the virgin deciduous forest to be uneven-aged and composed of all sizes of trees surrounded by abundant reproduction. In the constant competition for water, light, and the other necessities of life, only that reproduction survives which is physiologically and morphologically able to withstand adverse conditions until the death of a tree in the overstory releases it from suppression and allows it to take its place in the arborescent strata. Auten (1933) has demonstrated that the effect of such a virgin hardwood forest on the soil is to make it porous and water-absorbent through the effects of organic matter, soil fauna, and root channels. When a forest is cut off, the equilibrium of the factor complex is greatly disturbed. The porous, light forest soil is cultivated and mixed by the plow and, because of the absence of protective litter, is puddled by the impact of rain and a hard,

relatively impermeable crust is formed. The organic matter in the soil is subject to rapid oxidation, the soil fauna changes or disappears, and the result is a single-grained, relatively non-porous soil which has little resemblance to the highly developed forest soil.

It is in this degenerate state that the soil is turned back to nature. The typical abandoned field habitat is characterized by its exposure to direct sunlight and its poor physical soil conditions. These latter include low porosity, low water-holding capacity, and low absorptive power. All of these are more or less the result of the absence of organic matter and a plant covering. The effects of cultivation are still apparent in the well-defined furrows and the presence of the brown homogenous "plowed" zone at the top of the profile.

The first seed plants to invade this bare area are annuals such as *Syntherisma sanguinale, Sarothra gentianoides,* and *Leptilon canadense.* These enter during the first year after abandonment and are largely replaced during the second year by the annual *Ambrosia elatior* and the perennial *Aster ericoides.* Such an outstanding change in the vegetation within one year is an illustration of the previously pointed out unstable condition of the organismo-environmental complex in the early stages of secondary succession. Gradually, in the third and fourth years after the last cultivation, the annuals are replaced by perennials such as *Andropogon virginicus, Eupatorium hyssopifolium, Eupatorium capillifolium,* and several species of Solidago. The roots of these plants are able to penetrate the relatively compact surface soil and because of their perennial habit, can persist indefinitely when once established. Their roots seldom penetrate deeper than 10 inches and occur almost entirely in the brown "plowed" zone. Comparatively few roots are present in the herbaceous stage of dominance and, obviously, because of incomplete utilization of the soil by these roots, the habitat is not closed to further invasion. Simple correlation data between total thickness of the organic horizons and number of old field herbaceous species present through succession shows the highly significant figure of —0.973. Such a value denotes a high inverse correlation between number of these old field species and accumulation of organic debris. This inverse correlation is demonstrated graphically in Figure 16. The old field herbs persist, then, because the absence of litter enables their light seeds to reach mineral soil and when once germinated, root competition from the larger woody species is absent.

The pine, because of its wind-borne seed, is able to invade this type of herbaceous community and populate, more or less thoroughly, such areas with seedlings, the density of the stocking depending on proximity of seed trees, quality of seed year, and amount of organic litter which has accumulated under the tall herbs. Seeding-in of the pine continues until the young trees are several feet in height and a relatively thick covering of litter has accumulated over the surface of the mineral soil and until the root network characteristic of the pine stage is closed. Most of those pine individuals, which enter

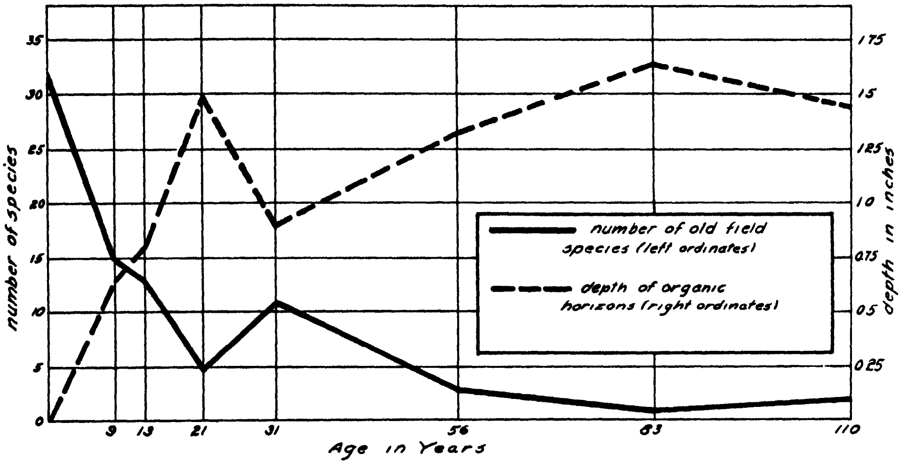

FIG. 16. Graphic representation of the inverse relationship between the total number of old-field herbaceous species and the depth of the organic horizons throughout the shortleaf pine succession.

in a dense stand after the oldest pines are taller than a few feet, never survive. From this it is evident that an even-aged stand is only approximately even-aged and occasionally individuals may vary as much as 10 years in age. From this point on, the discussion will refer only to even-aged stands which are fully stocked.

With the closing of the root network in the upper 6 inches of soil and the increase in size of trees, there is intensified competition for water, nutrients, and space. The result is a rapid decline in number of dominants as the weaker and more poorly equipped individuals die off. At the same time, the accumulated needle litter under the pines, coupled with the intense competition from the pine roots, tends to make the environment unsuitable for the old field herbs and these species are gradually eliminated. As pointed out previously, because of increasing depth of the pine litter, the light seeds of these herbs cannot reach mineral soil and so cannot germinate and become established. The high inverse correlation of —0.973 obtained between depth of litter and the presence of old field species seems to indicate one reason, at least, for the absence of such species in dense pine stands. The present results agree with those of Reed (1934) who found seeds of a great many old-field species of herbs in the organic horizons of the forest floor under shortleaf and loblolly pines. Only a few of these same species were represented in the herbaceous flora of the stands in which he worked. Kawada (1931) has shown somewhat the same thing in Japan, in that removal of litter from the forest floor under *Pinus thunbergii* results in a more xeric herbaceous flora.

The total depth of the organic remains increases rapidly at first and then more gradually as a stand approaches maturity. After a few years of occupation by pine, the decaying litter forms a zone of fermentation but it is not

until the stand is from 25 to 30 years old that the humus layer of broken-down organic matter appears. These last two layers tend to increase through succession while the layer of undecomposed litter remains practically uniform in thickness as the stand increases in age.

This accumulation of decaying and undecayed litter which adds organic matter to the soil is important in several ways. The data on thickness of these organic remains when correlated with those on water-holding capacity of the surface soil yield a highly significant correlation coefficient of 0.930. This correlation, which is graphically portrayed in Figure 17, is almost entirely

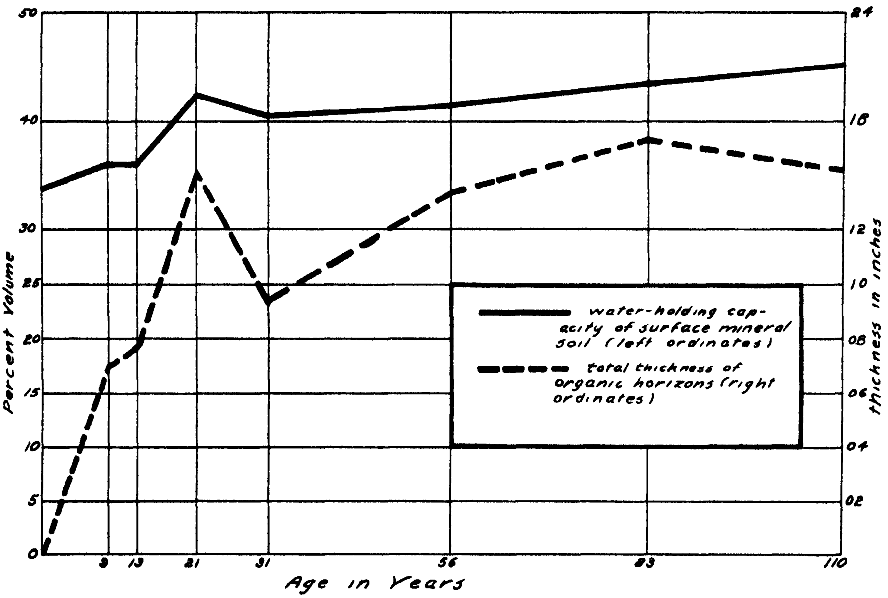

FIG. 17. Graphic representation of the positive correlation between depth of the organic horizons and the water-holding capacity of the surface mineral soil throughout the shortleaf pine succession.

dependent on amount of organic matter incorporated in the mineral horizons by leaching from above since, by reason of a coefficient of 0.884, water-holding capacity of the surface soil is shown to be highly correlated with its content of organic matter. Besides this effect on water-holding capacity through the addition of organic matter, the thickness of organic horizons also has a striking effect on reproduction of the key species of the pine-oak succession. Korstian (1927) has shown that because loss of moisture from acorns results in a great decrease in viability, a thick protective layer of litter is needed to preserve moisture necessary for germination. In the case of the present study, the first oak seedlings appear only after the pine litter has reached a depth of at least an inch. This depth is reached about the time that the stand is 20 years old. That the abundance of oak reproduction is largely governed all through the pine succession by depth of the organic remains, is

shown by the correlation coefficient of 0.639 obtained for these two factors with the present data. Although this coefficient is not statistically significant, it is large enough to suggest a positive effect of the organic horizons on reproduction of the several species of oak.

Aside from the protective influence of litter, the invasion of oaks is controlled by other factors. Water-holding capacity of the surface soil is one of these controlling factors. A simple correlation between this soil factor and density of oak reproduction shows a coefficient of 0.854 which statistically is highly significant according to Fisher's (1930) tables for the significance of values of r. Organic matter content in the surface soil is also highly correlated with the numbers of young oaks having a coefficient value of 0.805. Organic matter probably influences reproduction mainly in its effect on water-holding capacity and volume-weight of soil. The high correlation between organic matter and water-holding capacity has been previously pointed out and the coefficient of —0.911 shows a highly significant inverse correlation between organic content and volume-weight of the same soil. The effect of volume-weight itself on oak reproduction is readily brought out by the high inverse correlation coefficient of —0.879 between the two factors. Oak reproduction, then, seems also to increase as the soil becomes more porous and the soil of old fields and younger stands is too compact for easy penetration of oak radicles. This substantiates the results of Korstian (1927) who found that a compact soil was detrimental to the establishment of oak seedlings.

The combined effect of five of the most important edaphic factors on density of oak reproduction is shown when these six variables are subjected to multiple correlation. These five variables: thickness of organic horizons, water-holding capacity of surface soil, volume-weight of surface soil, organic matter of surface soil, and moisture equivalent of surface soil when correlated with the density of oak reproduction give a multiple correlation coefficient of 0.922. While this value is high, it is not a perfect correlation and there are other factors which might be considered as influencing the entrance and continued reproduction of oak. Since acorns are not wind disseminated and the areas under discussion are level, they can only reach the middle of a dense pine stand by being put there by animals. Squirrels probably eat most of the acorns which they bury in the litter but there are always some which escape this fate, and being naturally planted under this protective covering of litter, germinate and become established. Oaks, then, enter because the complex of factors which governs their germination and survival has been developed to a suitable point by a 20- to 30-year occupancy of old field sites by the pine community. In other words, they appear when the combined effects of root channels, fauna, and organic matter have made the soil moist and porous enough for their germination and continued survival. That this survival is also partially controlled by the morphology of oak seedlings will be pointed out later.

With this same increase in amount of litter, there is a sharp decrease in amount of pine reproduction. After a stand becomes approximately 30 years old, reproduction of pine is extremely rare. The result of this lack of reproduction, along with a decrease in the herbaceous flora before the oaks and other hardwoods are very numerous, is to give pine stands between the ages of 20 and 50 years a strikingly barren appearance as regards subordinant vegetation. Figure 3 brings out this barrenness of the forest floor quite clearly. There are probably several reasons for the failure of pine to reproduce under its own cover. A multiple correlation between density of pine reproduction and the same five edaphic factors which largely control oak reproduction yields a coefficient of only 0.601. Obviously there must be several other factors which partially control this disappearance of pine reproduction. In the first place, germination itself is probably considerably retarded by several environmental and morphological factors. Pine seed is very light and it is, therefore, unusual for it to penetrate through the increasingly deep litter and thus reach mineral soil. Barr (1930), working in British Columbia, found that spruce seeds failed to germinate when not reaching mineral soil because of inability of the seeds to absorb enough water from the highly hygroscopic humus. In shortleaf pine stands, failure of pine seed to germinate is probably the result of a combination of this lack of absorption of water with the possible detrimental effect of decreased light intensity.

If germination does take place, the seedlings seldom survive more than a year or two. On examining 1-year old seedlings of pine taken from the 31-year stand, it was found that the usual root system is extremely small, being only 1 or 2 inches long with one or two very short and weak laterals. Not much additional development occurs in the second year. This very poorly developed root system therefore penetrates to a depth of about 3 inches in 2 years' time. As has been shown, the root network closes early in the life of the stand and is almost entirely confined to the upper 6 inches of soil. It is evident from this that the poorly developed root of the pine seedling is in the zone of most intense competition. Craib (1929) has shown that during dry periods, trenched areas, in which the tree root competition is eliminated, have two to nine times as much available water in the first 6 inches of mineral soil as comparable untrenched areas. Toumey and Kienholz (1931) have conclusively demonstrated that this increased amount of available water during times of stress in the trenched areas, results in a very luxuriant herbaceous and low woody vegetation as compared to the barrenness of the usual forest floor with normal root competition. Similar studies reported by Korstian (1934) in the Duke Forest have shown comparable results. During dry periods there is undoubtedly no available water in the first 6 inches of soil due to its extraction by roots of dominant trees. This obviously results in the death of the seedling pine, since its weak, shallow root system occurs in the zone of most severe root competition.

While young pine reproduction fails to survive dry periods, the presence of numerous young oaks and other broad-leaved trees indicates the ability of these species to survive even though the surface soil is devoid of available moisture. The edaphic factors which condition the entrance and continued reproduction of oaks have been previously pointed out. However, why should oaks and certain other woody genera be able to survive through critical periods of soil moisture, while pine cannot, in spite of the obvious betterment of soil conditions? Morphological investigations on the seedlings of oak, hickory, tulip poplar, and red cedar in the 31-year stand reveal that these species all have uniformly strongly developed deep root systems when young. These observations agree with Toumey's (1926) findings that oak and hickory seedlings develop a 10- to 15-inch taproot the first year and that the red cedar and tulip poplar seedlings produce a deep, much-branched root system during the first year. In Figure 18, the root systems of one- and two-year old shortleaf pine seedlings are contrasted with those of a one-year old white oak and a three-year old black oak. Striking differences in depth of the root systems and also in thickness of the taproots are very apparent. The extensive root systems of tulip poplars two years old are illustrated in Figure 19. This figure shows the much-branched character of the root system of the seedling tulip poplar which aids greatly in the survival of this species under pine after once becoming established. The well-developed root system of a two-year old red cedar is shown in Figure 21.

Because these deeply penetrating root systems pass through and beyond the zone of greatest pine root competition, they survive the first season and considerably strengthen their position during the second year. This does not imply that they are entirely unaffected by the pine competition but they are, by virtue of their deeper root systems, better able to withstand periods of stress. Another characteristic in favor of the survival of these species is the ability to produce sprouts or new shoots from the base of the stem when the aerial parts are killed back by desiccation. This is especially true of oaks and tulip poplar. In Figure 19, the aerial parts of tulip poplar seedlings are two years old. However, the one with the largest root system exhibits the common characteristic of seedlings of this species to sprout and a new shoot has originated from the base of the dead stem.

Examination of the seedlings of red maple and dogwood, typical secondary trees, shows a highly developed, much-branched root system which would favor survival. The only shrubs examined were young individuals of *Viburnum rafinesquianum,* practically the only shrub present in the closed young pine stands. The root systems of this species are not only deep but also extremely thick and fibrous. The extensive fibrous root systems of young individuals of both Viburnum and Cornus appear in Figure 20.

Since these findings point to the fact that seedlings of woody species surviving pine competition must have either deeply penetrating taproots or a

highly developed fibrous root system during the first few seasons of growth, the question of herbaceous root systems arises. Since the herbs are rather rare in such dense pine stands, it is evident that most of them are not fitted

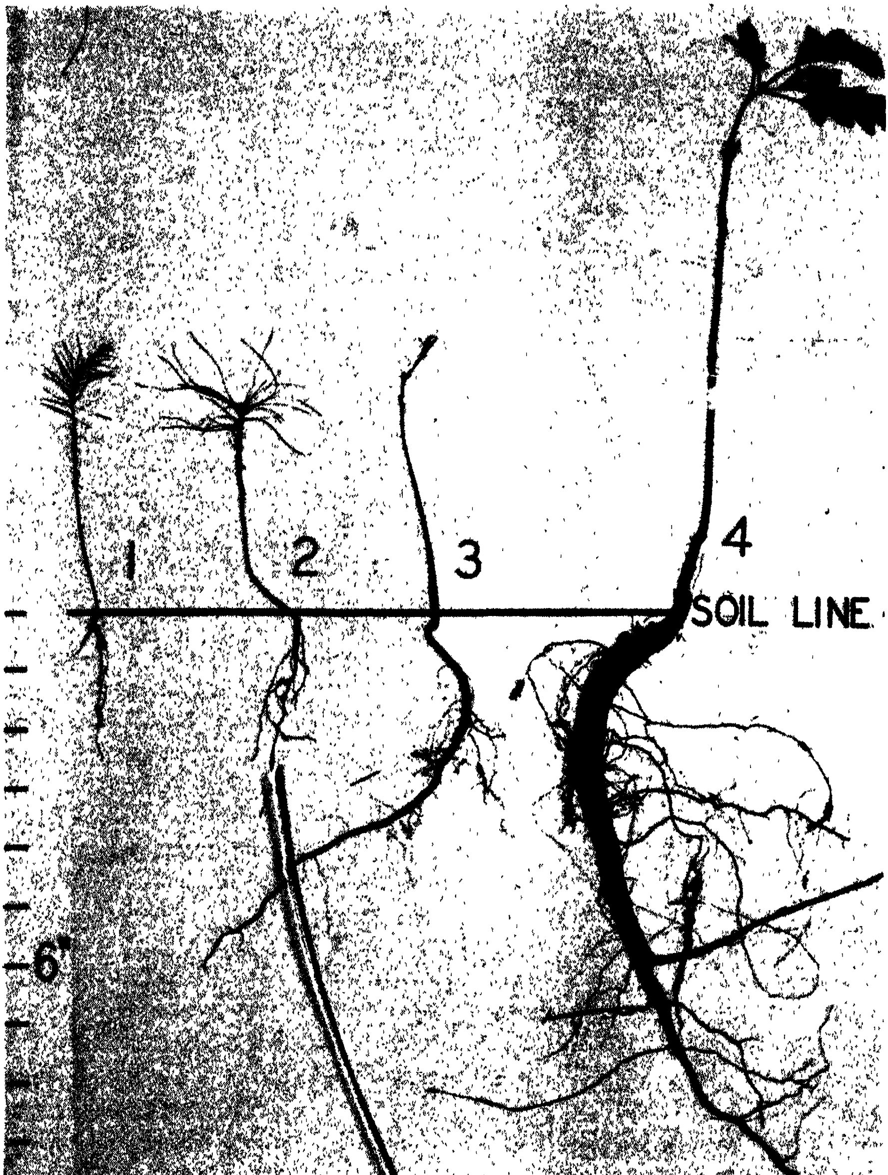

FIG. 18. Root systems of one-(1) and two-(2) year old shortleaf pine seedlings contrasted with the root systems of a one-year old white oak (3) and a three-year old black oak (4). All are from the 31-year old stand.

for survival even though germination takes place. The outstanding feature of the herbaceous flora is that it is made up almost entirely of perennial xerophytes. This bears out the assumption that the surface soil is extremely

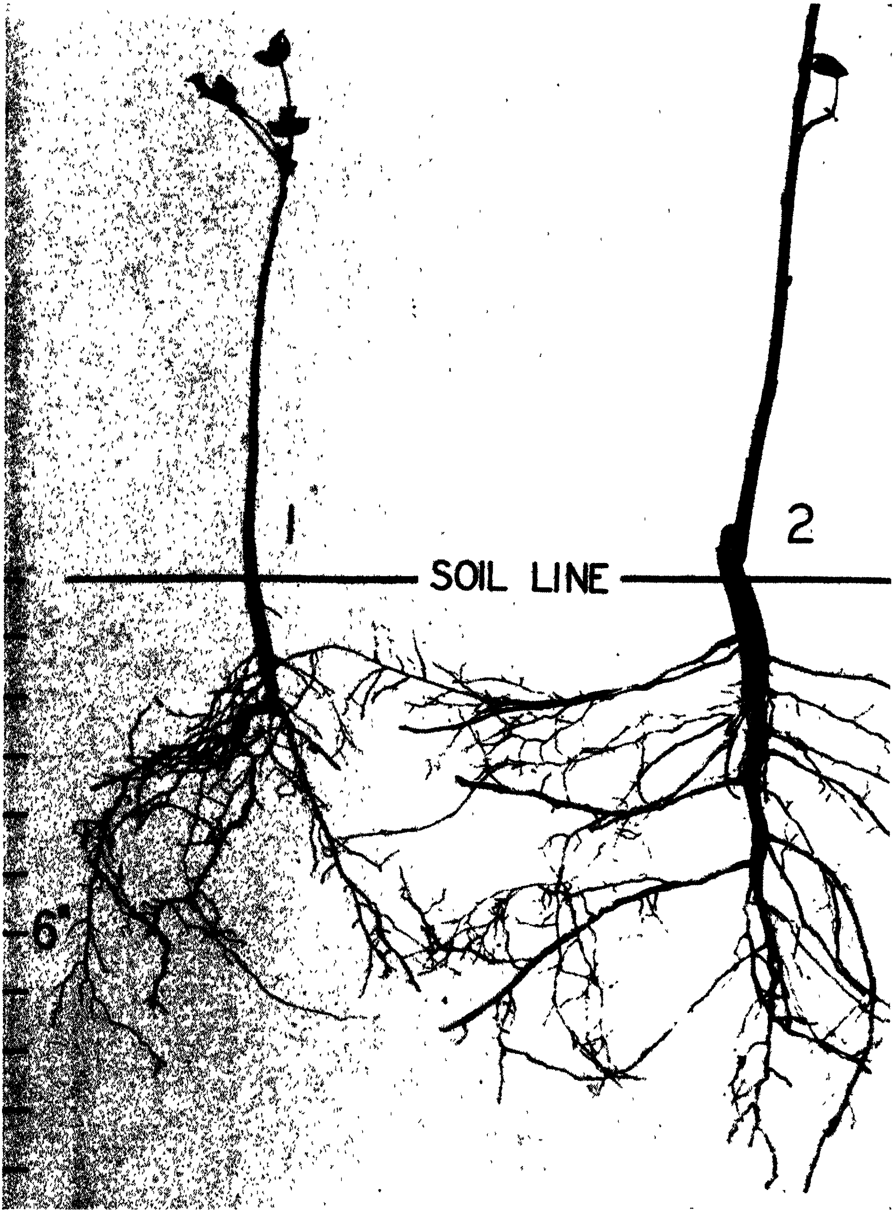

FIG. 19. Extensive root systems of two-year old tulip poplars. The one on the right has been killed back once and has sprouted from a dormant bud at the base of the stem. Both are from the 31-year stand.

dry at times as a result of root competition. The soil under a closed dense pine stand during the driest part of the year might well be compared to that of an exposed rocky ridge. It is powdery and probably entirely lacking in

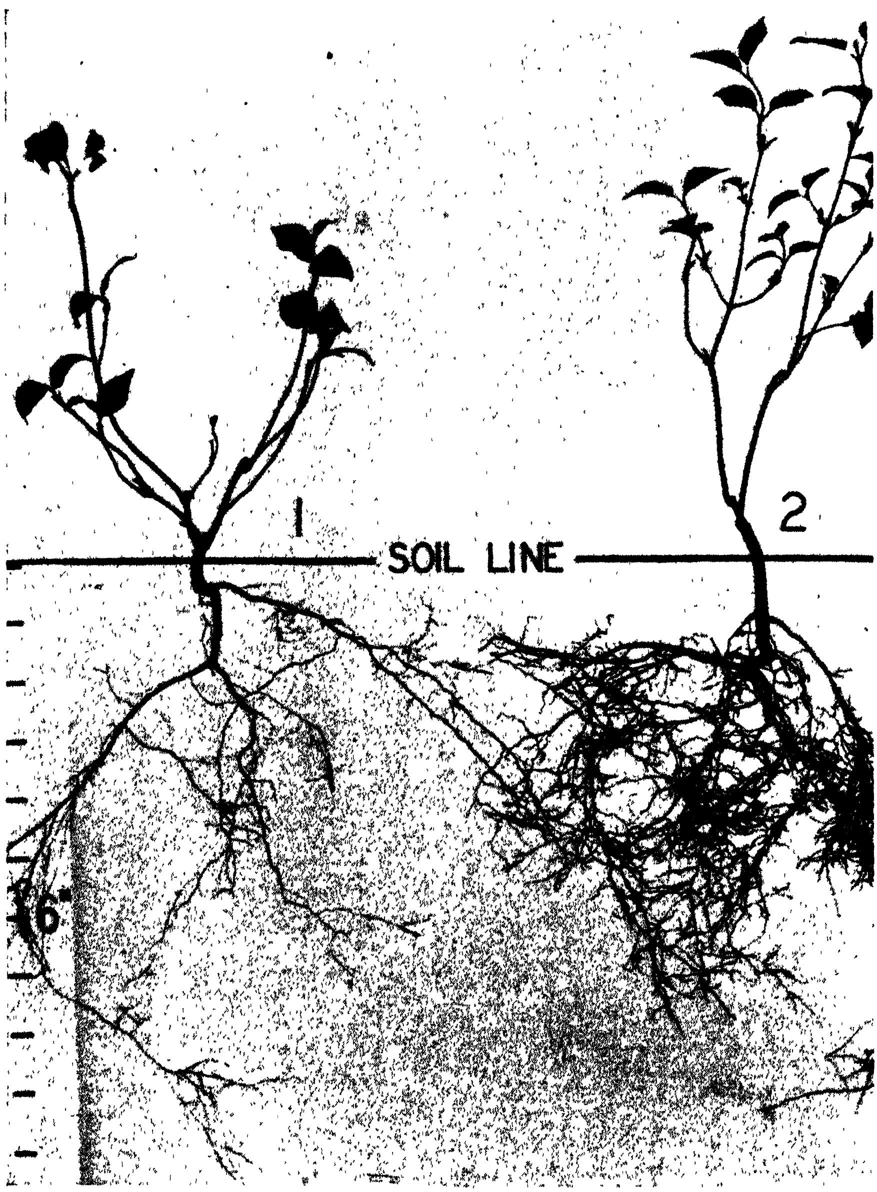

FIG. 20. Extensive fibrous root systems of flowering dogwood, *Cornus florida* (1), and downy viburnum, *Viburnum rafinesquianum* (2). Both are three years old and are from the 31-year stand.

available water. Some species, such as *Chimaphila maculata,* the most common herb in these stands, are heavily cutinized and evergreen. Others, such as *Elephantopus tomentosus* and *Gnaphalium obtusifolium* have the leaves covered with hairs. These characteristics result in decreased loss of water by transpiration and so physiologically fit the species for survival in such precarious habitats. The root systems of these plants are also fairly deep. The relation between depth of litter cover and number of old-field herbaceous species has been previously pointed out. Characteristically, the old-field species which survive and the typical pine forest herbs are perennials and reproduce vegetatively by means of stolons and underground stems. Because of these characteristics, many species can persist and spread in spite of the failure of their seeds to reach mineral soil. This is exemplified by *Chimaphila maculata, Gnaphalium obtusifolium,* and several species of Solidago. A mature plant of Chimaphila with underground shoots and deep roots appears in Figure 21.

About the same time as the first appearance of oak seedlings, the A_1 horizon begins to develop. It overlies the brownish "plowed" horizon and gradually replaces it. Because of its high content of organic matter which constantly increases, it has an increasingly high water-holding capacity, an active soil fauna, and a good crumb structure. The great hygroscopicity of humus is apparent from increased moisture equivalent of the surface soil as organic matter is added. The highly significant correlation coefficient of 0.949 between organic matter and moisture equivalent in this horizon bears out the dependence of a change in moisture equivalent on organic matter in the soil. This horizon gradually grows in thickness and from the addition of organic matter, the death of roots, and the activities of small animals becomes light and porous. This is an indication that the soil is beginning to return to its virgin forest condition.

As a pine stand approaches its middle age, the broad-leaved trees which have successfully become established, form a definite secondary arborescent stratum. Figure 9, an external view of an 85-year stand, shows this stratum of hardwood trees under the canopy of pine. The outstanding tree in this stratum is flowering dogwood which is always a secondary tree, rarely becoming dominant. Other trees, such as oaks, hickories, red maple, and tulip poplar, make up part of this understory. Almost all the species in this stratum also have abundant reproduction. The overstory pines die off gradually and with the death of each one, the understory hardwoods gain a distinct advantage. In the mature pine stand, the dominants are giving way to hardwoods as is shown by comparisons of frequency and density of the two groups. Figure 4, taken inside this stand, shows a few scattered old pines surrounded by a dense undergrowth of these hardwood trees. The surface root network of pine is still present but the increased abundance of deeper roots testify to the fact that oaks, hickories, and other deeply rooted species are firmly estab-

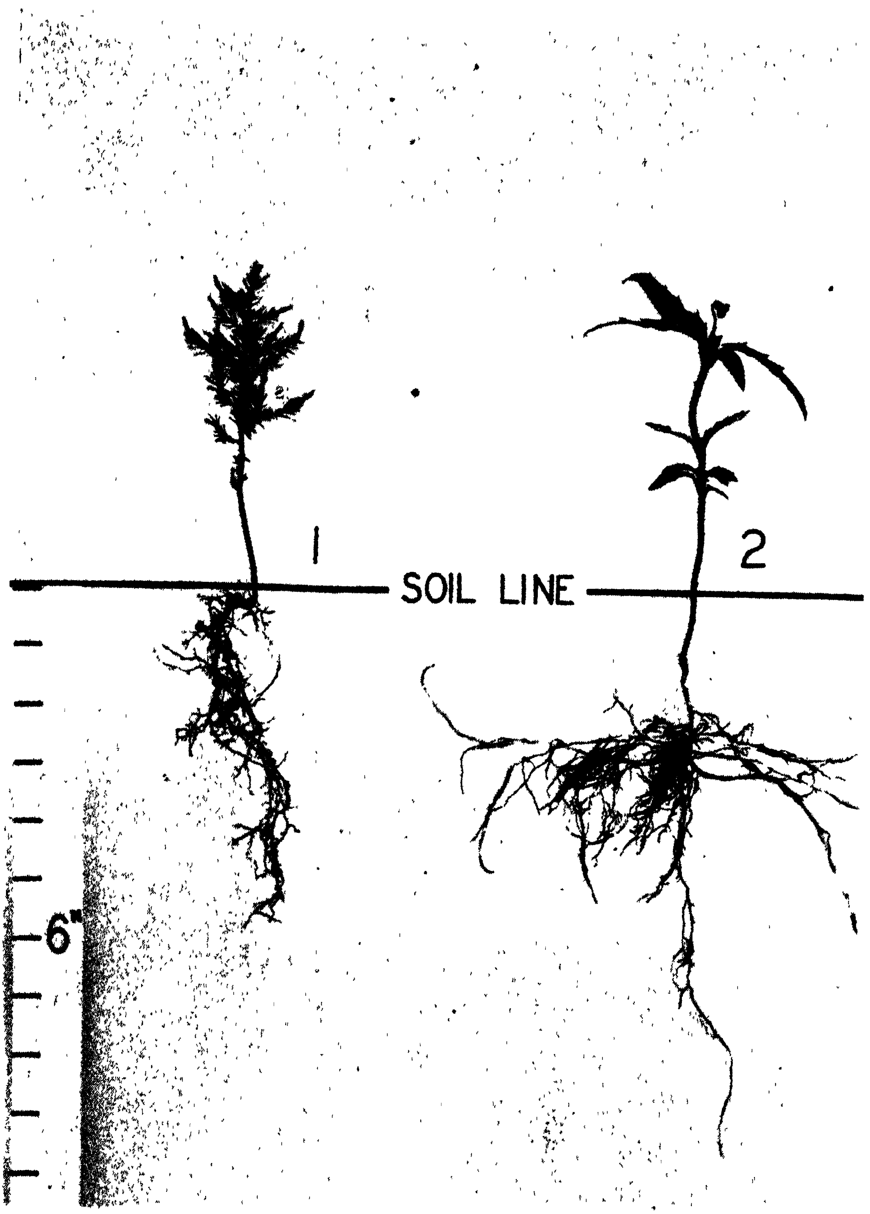

FIG. 21. Characteristic root systems of a two-year old red cedar (1) and a mature plant of *Chimaphila maculata* (2). Note the extensive rhizomes of the latter. Both specimens are from the 31-year old stand.

lished and that the soil will be utilized by roots to a much greater extent than in the pine stage.

Oaks and hickories are still only secondary trees in the mature pine stand but with the death of each mature pine, the nearest hardwoods are released from suppression and they rapidly assume dominance. Certain species, flowering dogwood, for instance, continue reproducing abundantly but never become more than secondary trees. It seems probable that these species make up a type of understory community which is dependent on an overstory but independent of the floristic composition of that overstory. If this is true, the dogwood synusia should continue on over into the hardwood community or phytocoenosis following pine. Observations on such hardwood stands reveal that this is the case and that this understory community is as well-developed there as it is in the pine phytocoenosis.

All through the pine succession, an herbaceous flora typical of hardwood stands has gradually been developing and by the time the pine is mature, this flora is fairly distinct and, with additions, continues over into the deciduous stand.

Pine, then, is a preliminary and temporary stage in the return to the climax forest. It is able to invade but, because of its own effect on the soil factors, especially those affecting soil moisture, is unable to maintain itself. However, by adding organic matter and by the formation of root channels, it prepares the soil for other species which successfully invade and eventually replace it by being better adapted to competition in the seedling stage and by utilizing the soil to a greater extent. Pine, through its effect on the soil, initiates the swing of the pendulum back toward a climax forest soil and the incoming hardwoods will continue this effect until sometime in the future the forest will again reach that near-stable organismo-environmental complex, the climax community.

SUMMARY

A quantitative analysis of the vegetation and certain soil factors was made on a successional series of shortleaf pine stands in the Duke Forest near Durham, North Carolina. These stands are on very nearly identical areas as regards climate, topography, and soils. The stands studied were limited to nearly level areas of a light-textured Lower Piedmont soil of good site quality. The vegetation was analyzed by means of several sizes of quadrats; a particular size being selected as best suited to the vegetation in any one vegetational stratum. Trenches were dug in each stand for the collection of soil samples for analysis. Soil studies included mechanical analysis, determination of amount of organic matter, moisture equivalent, water-holding capacity, volume-weight, air capacity, and profile development. The roots were mapped on vertical profiles by size classes. Studies were made of seedling root development of the more important species in the succession. The

results were correlated and integrated by the statistical method of calculating simple and multiple correlation coefficients between the several vegetational and soil factors. The important results are summarized as follows:

Vegetation.

1. Abandoned agricultural land on light-textured Piedmont soils is first occupied by a relatively shallow-rooted herbaceous community dominated by broom-sedge *(Andropogon virginicus)*.
2. Shortleaf pine invades these fields, often in great numbers, due to its wind-borne seeds.
3. Shortleaf pine is able to germinate and survive because of exposed mineral soil and low root competition.
4. Density of the dominant pines is very high when the stand is very young, in some cases averaging nearly 3,000 stems per acre. This density falls rapidly at first and then gradually levels off as the pines reach maturity and then lose their dominance. In the oldest stand studied, 110 years of age, there are only 60 pine stems per acre.
5. The closing of the network of pine roots, which through this stage of succession is mainly in the first 6 inches of soil (56 to 64 percent of the total roots as compared to 17 to 25 percent in the second 6 inches), occurs very early in the life of a stand. This, combined with the increasing depth of litter accumulating under pine, causes the disappearance of the old-field herbaceous species. A highly significant inverse correlation coefficient of —0.973 was obtained between depth of pine litter and presence of old-field herbs during succession.
6. The first oak seedlings appear at the time the stand is about 20 years old, when enough litter has accumulated to protect the acorns against loss of viability through desiccation and the surface soil has become porous and sufficiently retentive of moisture for their survival. The five most important variables affecting the entrance of oaks are: thickness of organic horizons and water-holding capacity, volume-weight, organic matter, and moisture equivalent of surface soil. These five factors, when correlated with the density of oak reproduction show a high multiple correlation coefficient of 0.922. The principal invading oaks are *Quercus rubra*, *Q. velutina*, and *Q. alba*.
7. Hickory reproduction does not enter until a few years after the first oaks appear. The principal hickories are *Hicoria alba* and *H. glabra*.
8. Pine reproduction declines rapidly in the younger stands and finally disappears altogether after the stand reaches middle age.
9. The barren appearance of the forest floor in the middle-aged stands is probably due to severe root competition from the dominant pines.
10. Pine seeds germinate only where they can reach mineral soil.
11. Once germinated, seedling pines under dominant pines seldom survive more than one or two years because of the very short, weak root system lying in the zone of intense competition from the dominant pines.

12. Surviving hardwood seedlings, such as those of oaks, hickories, and tulip poplar, persist because they develop either a long taproot or a much-branched fibrous root system during the first year. Many of these same species also sprout when killed back.

13. Most shrubs and herbs of the middle-aged pine stands also have well-developed root systems. The herbs are mostly perennial and usually reproduce vegetatively by stolons or rhizomes as exemplified by *Chimaphila maculata*.

14. A well-defined understory becomes evident by the time the stand reaches middle age. This layer is characterized by flowering dogwood and red maple and is present in the oldest pine stands and also in hardwood stands following pine.

15. An herbaceous flora characteristic of hardwood stands gradually develops as the pines grow older. This flora is typified by *Polygonatum biflorum, Peramium pubescens, Aristolochia serpentaria, Hexastylis virginica,* and *Viola* spp.

16. In mature stands, pine is beginning to lose out as is shown by its decreasing density and frequency. Each over-mature pine which dies is replaced by deeper-rooted hardwoods which its death releases from suppression.

Soils.

1. The surface soil in the herbaceous old-field community has a relatively high volume-weight (1.346), a low water-holding capacity (33.705 percent), a low organic matter content (less than 1 percent), and a low moisture equivalent (6.84 percent).

2. The profile of the soil occupied by this old-field community is characterized by a thick, brown "plowed" horizon at the top averaging about 12 inches in thickness.

3. The brown "plowed" zone grows thinner in an upward direction and is replaced by a blackish gray A_1 horizon which develops over it. This replacement occurs between ages of 20 and 30 years.

4. With the appearance of the A_1 horizon, there comes a decrease in volume-weight and an increase in water-holding capacity of the surface soil. The first is due to a combination of root channels, organic matter, and animals. The second is due mostly to the effect of increased organic matter and to some extent to greater porosity of the soil.

5. A progressive decrease in volume-weight and increase in water-holding capacity of the surface soil continues through the pine succession. The former averages only 1.029 in the mature stand, while the latter averages over 45 percent.

6. Through the addition of organic matter, there is also an increase in the moisture equivalent of the surface soil. A highly significant correlation

coefficient of 0.949 between these two variables shows the close dependence of any change in moisture equivalent upon a change in organic matter content.

7. No pronounced trend is exhibited by the air capacity of the soil during the pine succession, at least in the stands studied.

8. There seems to be no significant change in relative amounts of inorganic soil-fraction sizes during the pine succession.

9. The profile seems to be affected by pine only in the first 6 inches of soil. An A_1 horizon has developed in this region. This horizon becomes lighter and more retentive of water throughout the pine succession because of the addition of organic matter, the formation of root channels, and the activities of the soil fauna. These causal factors in soil change are conditioned by the presence of pine vegetation which in turn is changed and eventually disappears because of its effect on its own environment.

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ECOLOGICAL MONOGRAPHS

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A STUDY OF SOME ECOLOGIC FACTORS AFFECTING THE DISTRIBUTION OF PROTOZOA

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A STUDY OF SOME ECOLOGIC FACTORS AFFECTING THE DISTRIBUTION OF PROTOZOA

INTRODUCTION

Many of the lower organisms appear to have a truly cosmopolitan distribution; among such the protozoa are pre-eminent, whether they be soil dwellers or inhabitants of sea or fresh water. Indeed, many species have been recorded from both marine and fresh water habitats and it is a puzzle how they can so readily adjust themselves to such extremes of osmotic pressure, pH, and chemical environment as to dwell in each of the two situations. Finley (1930) has recently investigated the tolerance of 36 species of protozoa for as wide a range of environmental change as transferring them from their fresh water habitat to sea water. Four species stood a direct transfer, while 17 others adapted themselves to the new environment if the transfer was effected gradually, but ten per cent sea water was fatal to 11 species, while the remainder were tolerant of varying concentrations of less than 100 per cent. Yocom (1934) repeated this work on *Euplotes charon* and *E. patella* obtaining results contradictory to those of Finley.

I have transferred *Cyclidium glaucoma* directly to sea water, confirming the results of Finley with this organism. As Noland (1925) has pointed out, in the protozoa we are usually dealing with single cells set apart from their environment by nothing more than a thin pellicle and plasma membrane. Possibly the ready permeability and thinness of the protoplasmic body enable them to make quick adjustments. It is to be expected then that many protozoan species will exhibit a wide tolerance for environmental variations in light, temperature, hydrogen ion concentration, percentage of various salts, percentage of dissolved oxygen, the presence of various organic compounds, food substances, presence of other species and the like. Such a tolerance is indeed familiar to the more than casual student of these organisms, who notes that whenever and wherever he takes a sample of stagnant water for examination, certain species will almost invariably appear, while if he inoculates some of this material into laboratory cultures of the several infusions of hay, wheat, peptone or other media commonly used, there is a fairly definite succession of protozoan species, until the infusions finally approach a static condition wherein only an occasional active protozoon may be observed. These sequences and conditions have been recorded by Woodruff (1912), Fine (1925), and others. Nevertheless the list of commonly occurring species is sooner or later exhausted whether in a laboratory culture or field environment, and such additional forms as are thereafter found are thought of as "rare," i.e., restricted as to environment.

This cosmopolitan distribution applies to some of the rarely occurring species as well as the common ones. It is well illustrated by *Menoidium*

gracile, a large and sharply differentiated species which I found five times in the Muscle Shoals area and regarded as a new species until I was able to consult a paper by Playfair (1921) and found he had recorded it from Australia. Any search for factors governing the presence or absence of a given protozoan species in a given habitat at a given time, is difficult at best, but it is hoped that the accumulated data herein presented and discussed may be a contribution.

MATERIAL AND METHODS

In the past ten years I have examined several hundred plankton samples taken from a variety of habitats for the purpose of enumerating their protozoan fauna. Part of this work was done at the Oceanographic Institution at Woods Hole, Mass.; some in New Jersey; some in the Muscle Shoals area of Tennessee, Alabama and Mississippi; some at Reelfoot Lake in Tennessee; and some at Cincinnati, Ohio.

These habitats are shown in Table 1. Column 1 includes a wide variety of situations but all the others include more restricted environments. Imhoff tanks are digestion chambers, characteristically anaerobic and dark, receiving and digesting raw sewage; trickling filters and activated sludge chambers are likewise parts of sewage disposal plants, but well aerated.

The samples referred to herein were well mixed where taken and were examined soon after taking; if a long trip to the laboratory was necessary an iced container was used. In a few cases field examination of settled samples was made, but in most cases the water samples were centrifuged in 50 cc. tubes and the catch examined. All were fresh samples, no preserved ones having been studied.

Of course, not all the species in the samples were enumerated, nor were all those seen familiar to me. But only the most thoroughly examined samples are treated here, and the great majority of forms were either known to me, or were identified; probably only an occasional species was not observed.

THE NATURAL DISTRIBUTION OF PROTOZOAN SPECIES

Table 1 gives a list of protozoa occurring in eight general habitat types. Only those marine forms are included which are morphologically indistinguishable from fresh water species; for a more complete list of marine forms my paper (1936) on the Woods Hole protozoa should be consulted. This table does not consider either seasonal or light factors; except for the marine forms the samples were taken at various times of the year; all samples were taken in daylight.

A study of Table 1 will show that despite the widespread distribution of any protozoan species, there is probably a small chance of finding any given species in a chance habitat. A species may at times occupy a certain habitat in enormous numbers, as was the case with "Spirostomum Pond" at Woods Hole, or the familiar bloom of *Euglena sanguinea* on hot shallow ponds in the later summer, but such dominance is usually highly exclusive of other species and may be short lived. There are few protozoa which

might confidently be expected to occur in a random sample. In Column 1 only three species occurred in 50 per cent or more of the samples examined; viz., *Cyclidium glaucoma, Cinetochilum margaritaceum* and *Trachelomonas volvocina.* For these three organisms we may safely assume a tolerance of wide environmental changes, for they are inevitable in the habitats under consideration.

Perhaps the most evident fact shown by Table 1 is that some protozoa tolerate an enormous variation in environment. The habitats studied may be loosely divided into clean and polluted ones. Actually there are perhaps as many habitats represented as there are samples included by the table and only a few protozoa occupy most of the habitats sampled. Eighteen species occur in the four "clean water" situations, fourteen in all situations. Only four ciliates, *Chilodonella cucullulus, Colpidium colpoda, Cinetochilum margaritaceum* and *Cyclidium glaucoma* were found in such extremes as clean ponds, the ocean and the anaerobic darkness of an Imhoff tank; these same four successfully endured activated sludge to which sucrose had been added to a concentration of 12,000 p.p.m.

In one respect the table is misleading. Ninety-four species have been recorded from only one type of habitat, most of these appearing only in Column 1, and yet they are not necessarily rare. The testate rhizopods, for example *Nebela collaris,* are common in sphagnum bogs, not one of which was sampled in this study. Some species are common enough where they occur, as *Spirozona caudatum* which was an abundant ciliate during several months in the small Reservation Pool referred to below, but which I have encountered only once elsewhere. Other species are definitely rare; I have seen *Trachelius ovum* only once in my lifetime, yet it is a fairly large and unmistakable ciliate.

Certain protozoa may be looked for in certain types of loci, but be rare or lacking in others. Hausman (1917) listed some of these groups, recognizing environmental types of habitat by physical characteristics. If it were possible to break down the sampling stations of Column 1 to smaller groups we might gain an idea as to what sort of pool would probably yield certain species as *Rhipidodendron splendidum* or *Ophrydium versatile* or *Clathrulina elegans,* but we would be no nearer a determination of the factors responsible for its existence in such a situation. To get *Trimyema compressa* for study it is only necessary to pour raw domestic sewage into a tube sufficiently long so that anaerobic decomposition takes place at the bottom, and in a few days this ciliate will appear in the bottom sludge. These illustrations show that in a general way we correlate definite habitat types with particular protozoa or groups of protozoa but fail to recognize the specific factors favorable or restrictive to those places. It is evidently our lack of knowledge of these specific determinative factors that makes our correlations general, for despite the environmental variations shown to be tolerated in Table 1, only about 6 per cent of the species in Column 1 could be reason-

TABLE 1. THE LIST OF PROTOZOAN SPECIES IDENTIFIED FROM EIGHT TYPES OF HABITATS; SHOWING THE NUMBER OF TIMES EACH SPECIES OCCURRED IN THE TOTAL NUMBER OF SAMPLES EXAMINED

Species Present	*Frequency of Occurrence*							
	Ponds, pools or still areas along stream margins	Open waters of lakes	Tree or stump holes	Atlantic Ocean, Harbor at Woods Hole, Mass.	Polluted stream	Imhoff tank	Trickling filter	Activated sludge chamber
Total Number of Samples Examined	70	20	25	40	40	50	50	40
Sarcodina								
1. Acanthocystis aculeata	13	5	3					
2. Actinophrys sp.	7	1		3				
3. ” sol	16	2	1	2			1	
4. Actinosphaerium eichorni	8	1						
5. Allogromia fluviatilis	6	1						
6. Amoeba proteus	25	1			1		16	3
7. ” radiosa	16	1	2		1	1	7	1
8. ” striata	1				1	3	23	1
9. ” tachypodia	14				1		16	9
10. ” verrucosa	11	1				1	23	3
11. Arcella dentata	8	1						
12. ” discoides	6						2	
13. ” mitrata		1						
14. ” vulgaris	24	2	3		4	1	40	26
15. Astrodisculus radians	2							
16. Centropyxis aculeata	8		1				27	16
17. Chlamydophrys stercorea					1	3	18	5
18. ” minor					2	6	6	2
19. Clathrulina elegans	2			1				
20. Cyphoderia ampulla	1							
21. Cochliopodium bilimbosum					3	7	22	12
22. Difflugia acuminata							2	
23. ” corona	2						3	
24. ” globosa								1
25. ” lebes		5	1				2	
26. ” pyriformis	12	2	1				14	
27. ” urceolata	1							
28. Euglypha alveolata	8		2		2	12	12	5
29. ” ciliata	3							
30. Hartmanella hyalina‡	17	1	2	3	23	22	35	30
31. Heterophrys myriapoda	3						1	
32. Hyalodiscus rubicundus	2	1					1	
33. Lecquereusia modesta	1							
34. Microchlamys patella	1							
35. Nebela collaris	1							
36. Nuclearia simplex	7			1	1	3	18	23
37. Paulinella chromatophora	2							
38. Pamphagus mutabilis	3						3	
39. Pelomyxa palustris	6							
40. Pinacocystis fluviatilis	1			1				
41. Pseudodifflugia gracilis	2			1			1	
42. Quadrula symmetrica	1							
43. Raphidiophrys elegans	5						2	
44. ” pallidum	2	1						
45. Trinema lineare	11	1	1			2	11	2
46. Vahlkampfia albida	26		3		2	4	18	7
47. ” guttula	17				11	13	27	10
48. ” limax	20	2			8	11	22	17
49. Vampyrella lateritia	5	1						

(‡) Includes Dimastigamoeba gruberii; the two could not be distinguished in the trophic state.

TABLE 1. LIST OF PROTOZOAN SPECIES IDENTIFIED FROM EIGHT TYPES OF HABITATS *(Continued)*

Species Present	*Frequency of Occurrence*							
	Ponds, pools or still areas along stream margins	Open waters of lakes	Tree or stump holes	Atlantic Ocean, Harbor at Woods Hole, Mass.	Polluted stream	Imhoff tank	Trickling filter	Activated sludge chamber
Mastigophora								
50. Actinactis mirabilis			2					
51. Anisonema ovale	19	1	1	7		1	1	6
52. " emarginatum	2						2	
53. " truncatum				2			4	
54. Anthophysa vegetans	6	2			20	11	6	
55. Ascoglena vaginicola	1							
56. Astasia dangeardi	8		1				2	
57. " inflata			3				1	
58. " klebsii	2		1					
59. " ocellata	3							
60. Bicoeca lacustris	1	1						
61. Bodo angustus	4	1	2	1	8	8		1
62. " agilis					1	2		
63. " caudatus	1			3	5	20	8	2
64. " sp.	21	4						1
65. " globosus	8	2	3	9	5	2	4	1
66. " lens	16	5	1	2	2	3		1
67. " minimus	2		1		1	1		
68. " mutabilis	2				5	9		
69. " ovatus	1			2	12	17	6	2
70. Bodopsis godboldi					1	1		2
71. Carteria spp.	2	1			1			
72. Ceratium hirundinella		1						
73. Cercobodo crassicauda	3		1	2	5	8	3	1
74. " caudatus			1		9	18	4	2
75. " longicauda	2			3	6	17	9	3
76. " ovatus						3		
77. Cercomonas sp.	2							
78. " sp.					13	11		2
79. Chilomonas oblonga			5					
80. " paramecium	9	2	5	2	2	2	9	2
81. Chlamydomonas spp.	48	16	6	3	16	15	2	
82. Chlorogonium elongatum	2	1						
83. " euchlora	3		1	1	1			
84. Chroomonas cyaneus	2	3	1		2			
85. " nordstetii	2	1						
86. " pulex	9	3		1				
87. " setoniensis	11	3			2			
88. Chromulina ovalis	19	3						
89. " sp.		2	3		1			
90. Chrysamoeba radians	1							
91. Chrysapsis sagene	1							
92. Chrysocapsa plankton	1							
93. Clautriavia parva					6	16		
94. Codonocladium solitaria	1							
95. Codonosiga botrytis	3							
96. Collodictyon triciliatum	7	3		1	1		3	
97. Cryptochrysis commutata		3	2					
98. Cryptoglena pigra	2	3	1					
99. Cryptomonas erosa	28	11	4	1	3			
100. " ovata	27	11	2		6			
101. Cyathomonas truncata	29	1		1		1	3	2

TABLE 1. LIST OF PROTOZOAN SPECIES IDENTIFIED FROM EIGHT TYPES OF HABITATS *(Continued)*

Species Present	*Frequency of Occurrence*							
	Ponds, pools or still areas along stream margins	Open waters of lakes	Tree or stump holes	Atlantic Ocean, Harbor at Woods Hole, Mass.	Polluted stream	Imhoff tank	Trickling filter	Activated sludge chamber
102. Dinobryon acuminata	1							
103. " eurystomum	4							
104. " sertularia	7	1			2			
105. Dinomonas vorax				2	3	6		2
106. Distigma proteus	8		5		1	3	1	1
107. Entosiphon sulcatum	22				2	7	16	9
108. " ovatum	1		1					
109. Eudorina elegans	6	8			3			
110. Euglena acus	5	1			1			
111. " acutissima	6	1	3					
112. " deses	10				6	3		
113. " ehrenbergii	5							
114. " gracilis	15	1	3	1	1			
115. " intermedia						3		
116. " limnophila	1							
117. " mutabilis	7	2	1			1		
118. " pisciformis	28	5	2		4			
119. " polymorpha	28	3	2		5	5		
120. " proxima	1							
121. " quartana			1		9	2	3	3
122. " sanguinea	12	2						
123. " spirogyra	13	1						
124. " sociabilis	17	7						
125. " spiroides	1							
126. " terricola	1							
127. " torta	2							
128. " tripteris	3		1		2			
129. " viridis	30	3	1		11	1	1	
130. Gonium pectorale	16	7			4			
131. " sociale	1	1						
132. Gonyostomum semen	7	2						
133. Gymnodinium cyaneus	2							
134. " palustre	8	1						
135. Heteronema acus	4				1	2	1	
136. " globuliferum			1					
137. Hexamitus crassus	1		6		9	6	4	4
138. " inflatus					12	16	3	2
139. Hyalogonium klebsii			3					
140. Kephyrion ovum		3			2			
141. Lepocinclis ovum	12	2	4					
142. " texta	1				1			
143. Lobomonas rostrata	2	1			1			
144. Mallomonas spp.	23	9			7			
145. Mastigamoeba longifilum	1			4	13	18	3	1
146. " reptans	5		2		8	16	1	
147. Mastigella simplex	1				2	9		
148. Mastigina setosa	1							
149. Menoidium falcatum	1							
150. " gracile	5							
151. " sp.			6					
152. " incurvum	6		11		1	2	3	2
153. " tortuosum	1		1					
154. Monas amoebina	7	1		2	6	2	12	10
155. " minima	1				22	13	31	28

TABLE 1. LIST OF PROTOZOAN SPECIES IDENTIFIED FROM EIGHT TYPES OF HABITATS
(Continued)

Species Present	*Frequency of Occurrence*							
	Ponds, pools or still areas along stream margins	Open waters of lakes	Tree or stump holes	Atlantic Ocean, Harbor at Woods Hole, Mass.	Polluted stream	Imhoff tank	Tricklingfilter	Activated sludge chamber
156. Monas obliqua	3	..	.	..	11	3	11	12
157. " vivipara	4	2	2	4	1	2	8	5
158. " vulgaris	11	4	.		6	2	3	2
159. Monosiga ovata	2	.		1			1	.
160. " robusta	3	.	.					.
161. Multicilia lacustris	1	.	.	3				
162. Notosolenus orbicularis	21	2	2	5	2	23	12	9
163. Ochromonas variabilis	1	.	1	1	.			
164. Oicomonas ocellata	.		1				.	3
165. " obliqua		..	1					
166. " termo	7	2	.	3	23	5	17	11
167. " socialis	3	1		2	11	21	7	20
168. " steinii	8					2	1	1
169. Pandorina morum	11	15		.	3			
170. Peranema ovalis	8		1					
171. " trichophorum	25	1	1	2	5	4	30	31
172. Petalomonas carinata	10			3	2			
173. " mediocanellata		..		2	2			
174. " stëinii			1	..	1			
175. Phacotus lenticularis	2							
176. Phacus hispidula			1					
177. " longicauda	12		3					.
178. " lunularis	2				.			
179. " orbicularıs	3							
180. " pleuronectes	5	.						
181. " pyrum	11		1					
182. " sp.			1					
183. " stokesii	3		2		1			.
184. " torta	1				.			
185. " triqueter	15	2	4					
186. Platytheca micropora	.					1		
187. Pleodorina californica		1			2			
188. Pleuromonas jaculans	7	1	1	3	18	29	26	21
189. Polytoma uvella			2		13	8	3	1
190. Protochrysis viridis	1	1			.			
191. Rhipidodendron splendidum	3						.	
192. Rynchomonas nasuta	1	1			7	9	8	9
193. Salpingoeca marssoni						1		
194. Sphaerella lacustris	2							
195. Sphaerellopsis fluviatile	1							.
196. Spondylomorum quaternarium	.	.			1			
197. Synura uvella	17	2			6		1	
198. Tetramitus decissus	1	..			15	15	2	
199. " pyriformis	1	.	3		20	10	5	1
200. Thoracomonas phacotoides	4	4				.		.
201. Trachelomonas acanthostoma	1			.				.
202. " armata	7	1			.		.	.
203. " bernardi	1		.	.				
204. " conspersa	2	.			1			
205. " crebea	1	.				.		
206. " euchlora	12	1	1	1			.	.
207. " fluviatilis	1	..	.		.	..	.	.
208. " globularis	5	..	.		..	..		..

TABLE 1. LIST OF PROTOZOAN SPECIES IDENTIFIED FROM EIGHT TYPES OF HABITATS *(Continued)*

Species Present	*Frequency of Occurrence*							
	Ponds, pools or still areas along stream margins	Open waters of lakes	Tree or stump holes	Atlantic Ocean, Harbor at Woods Hole, Mass.	Polluted stream	Imhoff tank	Trickling filter	Activated sludge chamber
209. Trachelomonas hispida	24	6	6					
210. " horrida	1							
211. " intermedia	1							
212. " sp.	10	6						
213. " sp.			3					
214. " oblonga	4							
215. " obovata	1							
216. " orbicularis	1							
217. " raciborskii	1	3						
218. " reticulata	1							
219. " rugosa	1							
220. " rugulosa			1					
221. " spiculifera	1							
222. " triangularis		1						
223. " teres	3							
224. " urceolata	1	1						
225. " verrucosa	4	2	1					
226. " vermicularis		1						
227. " vestita	1	1						
228. " volvocina	43	8	8		7			
229. Trepomonas agilis	2		1	4	17	31	3	1
230. " rotans			2		22	10	2	2
231. Trigonomonas compressa	1		2		3			
232. Tropidoscyphus octacostatus	1			3				
233. Urceolus sabulosus	3			1				
Infusoria								
234. Amphisia (kessleri?)	4			1				
235. Aspidisca costata	18		1	5	3	3	31	29
236. " lynceus	7						6	5
237. " turrita				2			1	1
238. Balanitozoon agile	5		1		1			
239. Balanonema biceps	1							
240. Blepharisma lateritia	3							
241. " undulans	1		2				6	
242. Bursaria viridis	1							
243. Carchesium lachmanni					24	1	1	
244. " polypinum	5				3		2	1
245. Chaenia teres	2			2			2	
246. Chilodonella caudatus	1							
247. " cucullulus	20	2	4	5	8	3	27	11
248. " uncinatus	13						7	4
249. Chilodontopsis crenula	9							
250. Cinetochilum margaritaceum	36	4	3	4	4	6	10	9
251. Codonella cratera	2	5						
252. Coenomorpha medusula	6			12	2			
253. Coleps amphacanthus	1							
254. " hirtus	21	1			1		7	7
255. " octospinus	2							
256. Colpoda aspera			2		10	5	2	
257. " inflata	3				4	9	3	1
258. Colpidium campylum	3				9	1	2	5
259. " colpoda	3	1	4	2	7	6	8	3

TABLE 1. LIST OF PROTOZOAN SPECIES IDENTIFIED FROM EIGHT TYPES OF HABITATS
(Continued)

Species Present	*Frequency of Occurrence*							
	Ponds, pools or still areas along stream margins	Open waters of lakes	Tree or stump holes	Atlantic Ocean, Harbor at Woods Hole, Mass.	Polluted stream	Imhoff tank	Trickling filter	Activated sludge chamber
260. Cristigera spinifera	3							
261. Cyclidium glaucoma	37	7	4	15	14	6	32	30
262. Cyrtolophosis mucicola	3							
263. Dactylochlamys sp.			2		2			
264. Drepanomonas revoluta			3		3	1		
265. " sphagni	2							
266. " viridis	5							
267. Didinium nasutum	1						4	1
268. Dileptus anser	4						1	
269. " gigas	4							1
270. Dysteriopsis minuta					1	2		
271. Epistylis plicatilis					5		13	27
272. Euplotes charon	3			4			4	3
273. " harpa	3			2	1		9	3
274. " patella	3			2			2	1
275. " plumipes	1						1	
276. Frontonia acuminata	5							
277. " leucas	14	1		2				
278. Glaucoma frontata	5	1						
279. " scintillans	7				25	6	18	17
280. Halteria grandinella	17	8	6	4	1		1	
281. Hexotrichia caudatum					1	4		
282. Holophrya discolor	11		2	2	1			2
283. " nigricans	5	1						2
284. " ovum	2							
285. " sp.					12	13		
286. Lacrymaria coronata	4							
287. " olor	3			3				
288. Lagynus simplex	1		1		2		1	2
289. Lembadion bullinum	1							
290. " conchoides	9							
291. Lembus infusionum	5	1		3	2		4	1
292. " pusillus	1			2	1		1	1
293. Lionotus cygnus	1			1				
294. " fasciola	16		1	2	8	2	21	20
295. " lamella					6	2	7	9
296. " wrzesniowskii	6			1				
297. " sp.	16				2	6	8	11
298. Loxocephalus granulosus	16			4	3	1	3	1
299. Loxodes alveolata	1						2	
300. " magnus	1							
301. " rostrum	6	1		2			4	1
302. Loxophyllum maleagris					1		2	6
303. " rostratum	2		1					
304. Mesodinium pulex	8			3				
305. Metopus contortus	10				3	1		
306. " sigmoides	8		12		10	22	3	
307. Microthorax sulcatus	4		2		1		8	12
308. Nassula aurea	2		1	2				
309. " ornata	9			1				
310. Onychodromus grandis	1						1	
311. Ophrydium versatile	1							
312. Opercularia spp.					2	6	42	36

TABLE 1. LIST OF PROTOZOAN SPECIES IDENTIFIED FROM EIGHT TYPES OF HABITATS *(Continued)*

Species Present	*Frequency of Occurrence* Ponds, pools or still areas along stream margins	Open waters of lakes	Tree or stump holes	Atlantic Ocean, Harbor at Woods Hole, Mass.	Polluted stream	Imhoff tank	Trickling filter	Activated sludge chamber
313. Oxytricha chlorelligera	10	.	. .		. .	. .	.	. .
314. " fallax	12	2	3	1	6	2	13	3
315. " spp.	22	4	6	.	. .	.		.
316. Paramecium bursaria	4	.		.		. .	1	. .
317. " caudatum	10			. .	27	1	12	2
318. " putrinum	1	.	.	. .	5	3	8	1
319. " trichium	4	. .	. .	. .	.			
320. Plagiopyla nasuta	5			1	6	2	2	
321. Pleuronema chrysalis	3	.	.	1		1	4	.
322. Pleurotricha lanceolata	2				1		2	.
323. Prorodon griseum	2	. .		.		.	5	
324. " teres	4	. .	.	2			3	
325. Rhopalophrya crassa	1	. .	2				1	
326. Saprodinium putrinum	8	. .	5		12	28	1	
327. Spathidium spathula	4	1	1		1		3	7
328. Spirostomum ambiguum	8		.		5	.	2	
329. " teres	2		.	.	1	.	3	1
330. Spirozona caudatum	2				.			
331. Stentor coeruleus	9			.				
332. " polymorphus	13	1			2		7	.
333. Stichotricha secunda	2		. .	3	.		1	
334. Stylonychia mytilus	6	.	1	2	15		2	6
335. " pustulata	7				12		9	10
336. Strombidium gyrans	13	1	2		.			
337. Placus luciae	6							
338. Tintinnopsis fluviatile	1	. .			1			
339. Trachelius ovum	1	.		.				.
340. Trachelocerca phoenicopterus	2			5				
341. Trichopelma sphagnetorum	1				.			
342. Trimyema compressa			1	.	2	27	1	
343. Trochiliopsis opaca	. .	.	.		1	.	2	5
344. Urocentrum turbo	7	.		4		.	2	
345. Uroleptus piscis	1	.	.				5	
346. Uronema marina	13	.		3			1	
347. Urotricha farcta	12	3	.	.	1			
348. Vorticella campanula	5							3
349. " nebulifera		.	.	.		.		2
350. " microstoma	.			. .	20	6	8	17
351. " sp.	31	6	7	8		. .	26	10
Number species occurring:								
in each habitat	289	108	103	+	148	98	136	99
in 33% of samples	16	11	5	2	15	12	20	15
in all habitats	12	. .	.	. .		. .	.	
in first 3 habitats	41	. .	.	. .	. .	.	.	.
in last 4 habitats	57	. .	. .	.	. .	. .	. .	
in habitats 5 and 6	88	. .	. .	. .	. .	. .	. .	.

(+) Does not include any marine protozoa except those which have also been found in one of the seven freshwater habitats.

ably expected to occur as frequently as once in three samples of that type. For the perhaps less variable environment of activated sludge plants about 16 per cent of the species could be expected as often, at least in the active state. Table 1 emphasizes some of these general relationships to environment for the species considered by attempting to show frequency of occurrence correlated with numerous examinations of particular environments.

SEASONAL FACTORS

Temperature changes and changes in intensity or amount of light available for photosynthesis are difficult to separate from other seasonal effects. These include snow over ice on lakes or pools; increased volume of water in pool or stream by seasonal rainfall or melting snow, which diminishes organism concentration therein; shortening the age of water by rapid runoff following rainfall; and the manifold effects of erosion silt in flood waters such as changing chemical composition of the water, decreasing available light, or sweeping away a normal food supply. The seasonal variation in rivers or pools might be due to any one or combination of these effects. Actual proof of seasonal variation in numbers of protozoan species or individuals is quite rare in the literature.

Wang (1928) studied the seasonal distribution of protozoa in a pond in Philadelphia and listed a number of temperature effects, some of them direct. He decided that certain species were eurythermic, others thermophilic, and so on. His samples were from near the surface, however, and any stratification or nigration effects would have been missed.

Welch (1935) points out that disappearance of a plankton species may be only apparent, whereas the plankters are present in a body of unmodified water in some life history stage throughout the year and successive years. Interpretation of field results as directly due to temperature should consider the modification to which the body of water is subject. Kofoid (1903) found seasonal fluctuations in river plankton, deciding they were largely due to rapidity of multiplication as the temperature increased. Reinhard (1931) also noted some such fluctuations in the upper Mississippi, but they were minor changes affecting principally chlorophyll bearing forms. It need hardly be emphasized that extreme modifications are undergone by river waters. Examination of the Ohio in August and September, 1936, revealed an abundant plankton; *Cryptomonas erosa* occurring in all samples. But in January, 1937, this organism could not be found in the silt laden flood waters of the stream, whereas it was still abundant in ponds near Cincinnati.

Crozier and Harris (1922) found a seasonal fluctuation in the numbers of protozoa present in the Plainfield, N. J., trickling filter. This fluctuation may be entirely passive with the protozoa, and due to the well-known seasonal "sloughing" of the film from the stones. I have found no such changes in the somewhat similar protozoa of activated sludge plants, which maintain a high population throughout the year. These habitats are subject to con-

siderable less modification than streams, but their temperature ranges fluctuate markedly. Viehl (1934) has recently shown by experiments in activated sludge plants that temperatures between 8°C. and 35°C. produced hardly significant changes in numbers of species and organisms. His experiments ranged from 1.5°C. to 55°C. and only the lower and upper ranges were highly effective.

I believe the most marked seasonal changes due to temperature to be quantitative. In 1932 and 1933 I made some observations on a small pool in South Mountain Reservation near Milburn, N. J., and in 1934 Fronczak (1936) made a careful study of this pool from January 9th to April 30th. Its greatest modification in that time was largely due to temperature. This uncontaminated pool "20 feet long, and 5 feet wide at its widest part—17 to 18 inches deep in the center" is fed by seepage, and while occasionally flushed out by a rain or thaw, quickly resumes its normal appearance, so that its greatest yearly changes are probably those of temperature and an annual accumulation of leaves in the fall. Its pH remained close to 6.8 at all times and its iron content high. The first examination in the fall of 1932 showed 78 species, but 171 were recorded by Fronczak in his intensive study in 1934. During the time he worked the temperature ranged between 2°C. and 12°C., usually below 10°. There was constantly a large protozoan population present; often the water was green with chlorophyll bearing forms. At 2° there were 28,000 individuals per cc. comprising 40 species, 77 per cent being chlorophyll bearers. At a temperature of 4°, 175,000 per cc. were found. Numbers showed a definite rise as the temperature increased, but the number of species changed only slightly, and the summer species counts (mine) never exceeded those of winter; furthermore the summer and winter species list was about the same. The maximum number ever observed at one examination was 66, a winter count. During 3 years this pool showed no decided seasonal changes.

I have made substantially the same observations on a larger, spring-fed pond at Metuchen, N. J., where approximately as large a species list was obtained from beneath two inches of ice, when the temperature was about 4°C., as in late summer. Such observations indicate that seasonal effects must be very carefully evaluated.

There are undoubtedly certain species which react to high or low temperatures by encystment or some other alterations in the life history. Noland (1925) found certain ciliates which decidedly favored low temperatures and I have found this to be true of *Strombidium gyrans*. If the principal food of a protozoan species consisted of certain green flagellates, it might disappear except during the summer months when such forms as Pandorian or Gonium tend to be most abundant.

It is probable, however, that the majority of protozoa enjoy a broad range of temperature toleration if temperatures change gradually. It seems that the chief influence of low temperatures is to slow up metabolism, hence

division rate, while high temperatures accelerate it. I have proved experimentally that *Colpoda inflata* divided about three times as fast at 27°C. as at 10°C. Temperatures below 10°C. and above 30°C. probably greatly affect the numbers of individuals present, but not the number of species.

HYDROGEN ION CONCENTRATION AND CHEMICAL COMPOSITION AS LIMITING FACTORS

Table 2 gives a list of twenty-six species of protozoa found in a variety of habitats during two years work by Rudolfs and Lackey (1929) endeavoring to explain the breeding of mosquitoes in specific places. The most striking character of the data is the lack of any apparent correlation between the species found and the chemical composition of the water, the various factors noted. Indeed so wide are the ranges of pH, CO_2, CO_3, Cl, and SO_4 at which some of the species occur that one might be tempted to ask if those species are not possibly independent of these usually occurring environmental factors. For example, Saunders (1925), Pruthi (1927), Darby (1929), and Phelps (1934) have reported widely divergent findings as to the tolerated pH range for Paramecium and the optimum pH. Phelps was unable to account for the observed differences. Pruthi did not give the species of some genera other than Paramecium with which he worked, and different species of the same genus frequently react differently to similar conditions. Indeed much recent work of this sort has most unfortunately not given the species worked with, but only the genus. In a natural environment the pH may undergo extensive changes in relatively short periods of time, and if a species is unable to accommodate itself to these changes, it must die out or perhaps encyst; Peterson (1928) reports that suddenly lowering the pH from 7.4 to 6.5 by adding 0.5 per cent lactic acid "killed all of the active individuals and probably many of the encysted" *Euglena polymorpha*, but that after 18 days they reappeared, presumably from cysts, at a pH of 6.6 and thereafter adapted themselves to the medium, increasing greatly in numbers. In Table 2, 193 determinations have been made for 26 species of protozoa, and the lowest pH is 2.9 and the highest 8.0.

In an examination of another group of more than 200 field samples, *Trachelomonas volvocina* and *T. hispida* were found in 41. For these 41 samples the range of pH was 4.6 to 8.0; CO_2, .8 to 13.2 p.p.m.; CO_3, 1.0 to 297.0 p.p.m.; Cl, 0 to 40.0 p.p.m.; and SO_4, 0 to 1016 p.p.m. The maximum occurrence of these flagellates was at pH 6.4; but none were found at pH 6.3. If we plot their distribution and that of *Arcella vulgaris*, *Aspidisca costata*, *Cyclidium glaucoma*, *Halteria grandinella*, and *Oxytricha fallax* against the field pH records at which they were observed, no unimodal curve is obtained. Instead it is apparent that they occur at a wide range of hydrogen ion concentration; that a very large number of observations would be necessary to establish an optimum; and that the pH factor is probably inseparable from other factors.

TABLE 2. THE RANGE OF pH AND CERTAIN CHEMICAL SUBSTANCES IN FIELD SAMPLES CONTAINING VARIOUS PROTOZOA

Top figure the minimum, botton figure the maximum.
Results in parts per million

Organisms	Number samples in which found	pH	CO_2	CO_3	Cl	SO_4	Ca & Mg	Al	Tot. Sol.	Vol. Mat.	Fe
1. Actinophrys		2.9	2.2	0.0	0.0	0.0	0	0	tr	tr	0
sol	7	6.7	6.0	36.9	65.0	1644.0	0	99	tr	tr	85
2. Actinosphaerium		4.7	6.0	5.2	0.0	4.0	0	tr	tr	tr	0
eichorni	3	6.7	26.4	25.0	296.0	1570.2	0	...	.	...	tr
3. Arcella		2.9	2.0	0.0	0.0	0.0	0	0	tr	tr	0
vulgaris	20	7.4	44.0	225.7	19.84	1356.3	7	99	9	80	85
4. Clathrulina		5.4	3.5	9.6	7.95	10.0	...	....	...	....	.
elegans	3	6.9	9.6	19.2	972.0	65.7	.. .	..	. .	.....	..
5. Euglypha		4.2	0.0	2.6	0.0	0.0		tr	tr	tr	tr
alveolata	8	6.7	9.6	25.0	7.95	65.7	..	..	.	.	
6. Trinema		4.9	0.0	2.6	0.0	14.0	0	tr	tr	tr	0
lineare	5	6.7	9.6	25.0	7.95	48.0	.	...	. .	..	tr
7. Chilomonas		4.6	2.0	2.6	0.0	tr	.		tr	tr	..
paramecium	9	7.4	13.2	102.0	39.8	103.5	7	tr	110	80	tr
8. Entosiphon		5.9	2.0	8.4	0.0	80.0	tr	0	70	50	0
sulcatum	3	7.4	8.5	58.0	17.7	73.8	.	.	.	. ..	. .
9. Euglena		4.9	0.8	5.3	7.95	80.5	....	..	.	.	..
acus	3	6.9	10.5	27.7	11.7	159.8		..			
10. Euglena		2.9	5.2	0.0	tr	256.0	0	0	0	20	100
mutabilis	3	7.3	...	45.0	65.0	1636.3	0				85
11. Euglena		7.0	4.0	2.19	0.0	0.0	tr	0	0	100	0
polymorpha	6	8.0	11.4	135.0	91.0	935.4	18		680	640	18
12. Euglena		4.6	2.0	80.	0.0	80.0	0	0	70	50	0
viridis	5	7.5	11.4	6.0	29.7	1636.3	tr	45	.	.	18
13. Gonium		6.1	2.0	1.0	0.0	0.0	0	0	160	140	0
sociale	3	7.5	. .	135.0	tr	1016.0	800	tr	5200	4200	tr
14. Mallamonas caudata		4.6	3.5	3.3	0.0	41.0	..	.	.	. .	
var. macrolepis	6	6.4	26.4	21.0	45.6	1636.3	...	.	.	.	.
15. Menoidium		4.6	2.0	3.6	0.0	8.0	0	0	tr	tr	0
incurvum	6	7.5	135.0	58.0	7.9	259.7	tr	tr	520	420	tr
16. Peranema		5.2	2.2	4.5	0.0	14.0	0	tr	tr	tr	0
trichophorum	8	7.3	13.0	72.0	39.7	101.9	tr	.	680	640	tr
17. Rhipidodendron		4.9	1.7	9.6	0.0	tr	0	0	tr	tr	tr
splendidum	8	6.7	10.0	25.0	12.0	174.0	..	tr	900	600	....
18. Synura		4.9	0.4	2.6	tr	23.0	0	0	0	200	100
uvella	8	7.3	9.6	45.0	11.7	259.7	..	.	...	..	.. .
19. Aspidisca		4.6	0.0	2.4	0.0	70.0	0	tr	tr	tr	tr
costata	19	7.3	15.8	153.6	65.5	36638.0	tr	580		...	120
20. Chilodonella		4.8	2.0	1.0	0.0	0.0	0	0	tr	tr	0
cucullulus	7	7.4	29.9	229.6	60.0	2038.0	7	tr	7000	5000	tr
21. Coleps		5.5	2.0	6.0	tr	0.0	tr	0	70	100	0
hirtus	7	7.4	29.9	229.6	60.0	2729.0	70	tr	110	80	..
22. Cyclidium		2.9	0.0	0.0	0.0	0.0	0	0	110	60	0
glaucoma	11	8.0	9.6	219.0	91.0	256.0	18	9	900	160	85
23. Frontonia		4.6	2.4	3.6	0.0	0.0	0	0	tr	tr	0
leucas	5	7.5	9.6	25.0	7.9	208.0	114	248	. .	. .	52
24. Halteria		4.2	2.6	2.4	0.0	0.0	0	0	90	60	0
grandinella	11	7.5	28.1	225.7	29.0	1636.3	tr	172	..	.	tr
25. Microthorax		5.8	2.2	6.0	0.0	14.0	0	0	0	tr	tr
sulcatus	5	8.0	6.0	297.0	7.9	108.5	13	tr	tr	24	18
26. Oxytricha		4.6	2.0	2.4	0.0	0.0	tr	0	70	50	0
fallax	14	7.5	29.9	53.6	91.0	2729.0	18	tr	6800	6400	tr

Noland (1925) has made similar observations on *Aspidisca costata, Cyclidium glaucoma,* and *Halteria grandinella.* His alkaline values exceed those recorded here in each case; 9.8 for Aspidisca and Halteria; 8.6 for Cyclidium. He did not note an optimum pH for any of the three, either in the field or in laboratory cultures, but averaged the pH values and concluded that "it is doubtful whether the pH exerts any direct influence on ciliate distribution within the range observed." This assumption is in complete accord with the results of this survey as far as the twenty-six species herein dealt with are concerned.

Such a conclusion might well be applied to the chemical values shown by the analyses. Wide ranges of CO_2, CO_3, Cl, and SO_4, are found to be tolerated. If any inference is to be drawn from the data, it is probably that the species concerned are independent of the limits of the above chemical factors likely to occur in stagnant water. This is borne out in part by the fact that 13 of the 26 organisms in Table 2 were found by Edmondson (1920) in Devils Lake waters, where the salts concentration approximates that of the sea, but with very high sulphates rather than chlorides; and that 10 of these 26 species were found in the Atlantic Ocean. Kofoid (1903) found that there was little correlation between chemical changes and seasonal fluctuations of the plankton in the Illinois River, and Weston and Turner (1917) noted that a sewage-polluted stream returned to a normal biological condition before its normal chemical condition was restored.

The 41 samples in which *Trachelomonas volvocina* and *T. hispida* occurred were taken from 12 stations over a period of two years. Despite extensive variation of the chemical makeup of the pools the organisms persisted. Fine (1912) is of the opinion that extensive knowledge of the chemical makeup of the environment would still produce only the most superficial correlations, and he shows that either titratable acidity or protozoan sequence may vary widely in hay infusions without appreciably affecting the course of the other, and a study of these data apparently indicates that such is the case for these two organisms.

The wide variations in amounts of salts and radicals present in the sample suggests that a balance is produced in the environment between various salts and radicals, and it is this balance which enables the protozoa to be tolerant of wide fluctuations in pH range.

Temperature variations, dissolved oxygen, light intensity, and such factors are not necessarily significant, for the 41 samples were all from natural pools, streams, or ditches. In general the chemical analyses justified the pH values and indicate that there were no large quantities of other, possibly toxic, ions present. Some conspicuous exceptions occurred as in sample 19, where there were small values for CO_2, CO_3, and Cl, but the highest recorded value for SO_4, 259.7 and a pH of 5.5. It is not known what other salts were present to aid the balancing action, but there were numerous protozoa of

nine species in this water, strengthening the argument that the buffering action of the salt balance accounts for wide tolerance of pH.

FOOD AS A LIMITING FACTOR

Sandon (1932) believes that food is largely the controlling factor for protozoa. If so, one might reasonably expect a large variety of bacteria-eating protozoa to be present in the aeration chambers of a sewage disposal plant or in its trickling filters. Table 4 gives a list of species exceeding 100 per cc., and numbers present in the aeration chambers or trickling filters of three disposal plants on several dates. The numbers of individuals are large, but numbers of species disappointingly small, even if those occurring in small numbers be added. Paramecium is usually absent from the samples at the Cincinnati and Tenafly plants although one or more species may occasionally be found in them and in nearby polluted waters. Yet there are bacteria present which Phelps (1934) and others have shown to be food for it. There is abundant oxygen, air being continually forced through the sludge. The pH values are constantly near neutrality and no large quantities of trade wastes are present. Any attempted conclusion from this table would be exactly counter to the idea that food is the limiting factor, for here where there is an abundance of it, other factors tend to sharply restrict the protozoan fauna. *Strombidium gyrans* feeds largely on *Chromulina ovalis*, and when the numbers of these drop in the Reservation Pool, Strombidium also becomes scarce, but such an observation is not proof of cause and effect. It has been stated that the abundance of organisms of one type found in a given situation is in a general way inversely proportional to the diversity of kinds, but there is perhaps the potential for supporting an enormous population in these three sewage disposal plants; yet neither in types nor numbers of individuals do the protozoa seem to approach their limit there. The Plainfield disposal plant over a period of time contains a much greater number of species in its trickling filter, as shown by Table 1, Column 7. This list is incomplete, not all the species of small flagellates having been identified; also some species which occur only once or twice in a year are not given in the table, but it certainly includes those which occur with significant frequency. Apparently all sewage disposal plants which treat largely domestic wastes have approximately the same fauna. Lists of protozoa occurring in other New Jersey disposal plants as Chatham, Red Bank, Barrington and Collingswood have shown substantially the same organisms, while similar faunas are reported from Decatur, Illinois, by Agersborg (1929); from Leipsic by Viehl (1934); from State College, Pa., by Lindsay (1930); and Ames, Iowa, by Frye and Becker (1929). Total numbers may vary considerably in different plants and at different times, but the species list does not vary a great deal. While the list includes many common species, it also includes some species rarely found elsewhere; on the other hand a number of species common to natural waters or stagnant pools are not found in such

plants, as will be seen by comparing Columns 7 and 8 with Column 1 in Table 1. This fact and the wide occurrence of similar species in sewage disposal plants might indicate that such plants offer an environment whose limits are well fixed. Decided variations occur within these limits, but a balance is maintained, and the organisms are largely independent of the fluctuations as far as existence is concerned. If in addition to their domestic wastes, large quantities of alkalis, acids or trade wastes of various kinds are introduced into the influent, the numbers and kinds of the protozoa will be greatly affected, and the efficiency of the plant possibly impaired.

Since there is certainly an abundance of food for bacterial feeders in trickling filters and activated sludge chambers, as is indicated by the great reduction of bacteria in these places, it might be expected that pH or chemical substances would account for the differences in fauna. Such is not the case; sewage is normally a very dilute mixture, and in aeration chamber or trickling filter normally contains abundant dissolved oxygen, while its pH and chemical composition are comparable to the field water samples analyzed in Table 2. And yet its most characteristic protozoon, Opercularia, was not recorded once in the 68 field samples of Table 1, while other faunal differences almost as great exist. Evidently its organisms manifest highly specific food requirements, or it possesses minute quantities of restrictive decomposition products; or its physical characteristics as a substrate are restrictive.

Where an organism is a highly selective feeder as *Didinium nasutum* which feeds on Paramecium, food can easily be a controlling factor. But where feeding is not selective, as seems to be the case with so many protozoa, food ceases to be restrictive.

POSSIBLE LIMITING FACTORS IN IMHOFF TANKS

In sewage disposal plants, both sprinkling filters and aeration chambers contain quantities of putrescible matter and large numbers of bacteria, so that both saprozoic and holozoic animals should thrive. One not acquainted with methods of sewage disposal might suspect oxygen depletion or hydrogen sulfide accumulation as limiting factors. Neither applies to these parts of a plant, however, because air is intentionally supplied in both cases. In Imhoff and septic tanks there is typically no oxygen and there may be H_2S; putrescible matter and bacteria are very abundant here also. But the protozoan fauna is very limited both as to numbers of species and numbers of individuals. Column 6 of Table 1 is a list of the species found by me (1925) in some numbers in the Imhoff tanks at Plainfield, N. J., and other places. These may not be present at all times and it is rare that they reach high numbers, but four species of ciliates, eight species of flagellates, and one rhizopod occur with some constancy in the tanks. These 13 species are different from those of the filter beds and their numbers are small. Careful studies of these tanks (1926) indicate a fauna which rarely exceeds 20,000 per liter, when the tanks are functioning normally. Extreme variations occur

when they function poorly, but their fauna may dwindle practically to the vanishing point, a condition which never occurs in the filter beds or in the aeration tanks. The tank protozoa therefore constitute a group very restricted by environment. Experiments (1932) have shown that they are either facultative or obligatory anaerobes. For the latter the presence of oxygen is a limiting factor. *Trepomonas agilis, Metopus sigmoides, Saprodinium putrinum, Trimyema compressa,* with a small unidentified Holophyra are certainly in this category, and probably *Hexamitus inflata* and *Mastigella simplex*. These thrive in Novy jars from which the oxygen has been exhausted. But if H_2S accumulates, Metopus will die out, while the remaining four endure considerable concentrations of this gas. None of the other Imhoff tank forms listed exhibit any marked tolerance for H_2S, and while some of them will thrive in Petri dish cultures under a thick film of paraffin oil floating on the water, if the oil seals the dish tightly by forming a film between the rim and the cover so that H_2S accumulates they quickly die out.

Many protozoa appear to stand some degree of oxygen depletion. I have grown many species under films of paraffin oil during the last three years; *Entosiphon sulcatus* grows in enormous numbers whether with or without the film of paraffin oil, but no mass cultures of *Distigma proteus* were procurable except in media under a cover of paraffin oil despite the fact that this organism is occasionally met with in the field. Thriving cultures of *Holosticha rubrum,* a large red marine ciliate, have been maintained for six months, with the best cultures growing under oil. Coste (1917) has shown that oils do not exclude oxygen from water and while oxygen is more soluble in petroleum (paraffin oil) than in water, (.028 volumes per volume of water, as compared to .202 volumes per volume of petroleum at 20°C.), there is apparently a small transfer of oxygen across the surfaces in contact, the oxygen below soon being partially depleted.

Oxygen exhaustion, then, seems to be a limiting factor if sufficiently great; a high percentage of H_2S seems to be another. In the field, however, these two conditions are rarely met. Noland (1925) noted that *Colpoda steinii, C. cucullus, Glaucoma scintillans, G. pyriformis,* and *Paramecium caudatum* were tolerant of a very low oxygen content. Of these only *G. scintillans* has ever been met with in the Imhoff tanks, although the others can be cultivated in infusions under paraffin oil. Evidently they are not tolerant to H_2S or more probably methane. Although albumen digesting bacteria (H_2S producers) are present in the tanks the concentration of H_2S in the tank gases is usually not greater than 0.1 per cent. Methane is usually about 70.0 per cent; CO_2 20.0 per cent to 25.0 per cent and sometimes CO about 0.3 per cent in the tank gases. Under acid conditions, the tanks foam and small amounts of hydrogen appear. When this occurs, very large numbers of small flagellates, principally *Trepomonas agilis,* but also some *Tetramitus decissus* and *Hexamitus inflatus* make their appearance. The hydrogen can hardly be called the stimulus here, but the lack of oxygen

TABLE 3. LIST OF PROTOZOAN SPECIES WHOSE NUMBERS APPROXIMATED OR EXCEEDED 100 PER CC. IN THE TRICKLING FILTERS AND AERATION CHAMBERS OF THREE SEWAGE DISPOSAL PLANTS

Organism	Plainfield, N. J. Trickling filter[1]						Tenafly, N. J. Activated sludge						Cincinnati, Ohio Activated sludge			
	9-9-22	1-1-23	5-5-23	10-2-24	10-5-24	11-7-24	7-8-33	7-10-33	7-12-33	7-26-33	8-1-33	8-31-33	8-3-36	8-24-36	8-31-36	9-18-36
Sarcodina																
Amoeba spp.(2)	1000	2000	1500	9700	2200	4000	18000	13200	28100	64400	61400	13000	300	1500	700	500
Arcella spp.	4000	2000	3000	4700	6500	7000		200	200	200	200	200	2300	400	100	600
Chlamydophrys stercorea										300			100	400		
Centropyxis aculeata						700							100			100
Cochliopodium bilimbosum								200					4300		200	
Difflugia pyriformis and lebes	1000	2000	100	400	2900	1000					100					
Euglypha alveolata and ciliata	1500		2000	5000	1400	600							300	100		
Nuclearia simplex						5000							100		1500	
Trinema lineare				1100									100			
Mastigophora																
Anisonema ovale													2900			100
Distigma proteus				400			400									
Entosiphon sulcatus					100				200				400		300	
Euglena sp (3)				400	100	1000			200					100		
Peranema trichophorum				200	500	500	1200	400	600	400	200		500	700		100
Minute flagellates(4)	15000	30000	20000	63300	67000	18000							100			100
Infusoria																
Aspidisca costata	1000	8000	1000	4700	5800	4000	9200	7700	6700	9600	10700	200	300	1500	700	500
Blepharisma undulans				400												
Chilodonella cucullulus	200	1500				300								600	100	100
Chilodonella uncinatus					1400											
Cinetochilum margaritaceum														200		
Colpidium campyla		5000		1400	1000					600		200				
Colpoda sp.	1000	5000	1000													
Cyclidium glaucoma															100	100
Frontonia leucas					700											
Holophrya nigricans	1000	1000														
Lionotus fasciola				3300	13000	600		200	200		200	200				
Lionotus sp.				58800		1200	800	1000	2100	1500	200	200	100	1500	1700	1500
Loxophyllum rostratum	1500															
Opercularia spp.(5)	80000	70000	50000	96600	108000	70000	2300	7800	10400	8800	13600	13000	1300	6300	1400	4500
Oxytricha fallax					500	100										
Paramecium caudatum	3000	30000		400		1000										
Paramecium putrinum					700			400								
Pleuronema chrysalis					700											
Spirostomum ambiguum		100	100													
Stylonychia pustulata	100	2000				1300			200					100	100	
Vorticella spp.	100	1000	3000	400		300							2200			600
Acineta grandis							800	1700	800	600	200		200			
Podophrya fixa											100			100	100	

(1) Hausman gives only genera: species given I subsequently found at Plainfield.
(2) Includes four species Amoeba and three of Vahlkampfia.
(3) Colorless, either gracilis or quartana.
(4) Several genera, but in hasty counting no careful identification can be made.
(5) Includes also some species of Epistylis.

and the presence of the other gases certainly combine to restrict the fauna to the organisms noted.

ASSOCIATIONS

Despite the apparently cosmopolitan distribution of many protozoan species, any particular habitat is likely to be characterized by a certain group of protozoa whose occurrence therein is determined by a number of environmental factors including possibly associations of certain organisms. The food associations of *Strombidium gyrans* with *Chromulina ovalis* or *Didinium nasutum* with *Paramecium caudatum* are of this nature. But more evident groupings are encountered if one studies a certain habitat over a period of time. The Reservation Pool studied by Fronczak (1936) and myself, showed practically the same list of species in 1932, 1933 and 1934. Many of these occurred sporadically but the bulk of its population, at times a very large one, was made up of about 60 constantly recurring species. Sixteen of the organisms of Table 2 and 18 of those in Table 5 occurred almost constantly in it. But whereas only 6 per cent of the protozoa in Column 1 of Table 1 might be found in one out of three random samples, 42 per cent of the species from this pool were found in one third of the samples, i.e., there was a marked association of species. The practically constant occurrence of organisms such as *Chromulina ovalis, Chroomonas setoniensis, Strombidium gyrans, Balanitozoon agile, Oxytricha chlorelligera, Dileptus gigas, Glaucoma frontata, Placus luciae* and *Spirozona caudata* is noteworthy, for most of these organisms do not occur commonly, and rarely together, so far as my field experience indicates. While such constant associations may be readily recognized, they give little indication of causative conditions, but they do point to a relative sameness of those causative conditions.

PROTOZOA AS ECOLOGIC INDICATORS

From a study of the data presented herein, some conclusions may be drawn as to the value of certain protozoa for indicating the degree of pollution of natural waters. Kolkwitz and Marsson (1909), Forbes and Richardson (1913), Purdy (1922, 1930), Noland (1925), and others have already classified many species ecologically in respect to pollution, and Whipple (1927) gives a table of the species so classified.

Pollution usually means the presence of sewage, but it might mean the presence of offensive odors and tastes, a high *B. coli* count, depletion of oxygen saturation, or a combination of these, from other causes. To be valuable as indicators of purity, a protozoan species should not thrive under oxygen depletion or extremes of pH; it should be quite susceptible to unusual salts, gases, or organic substances in the water. Some organisms will occur in too great numbers under a variety of conditions to be indicators. *Euglena polymorpha* occurred abundantly in 1924 at 6 stations under the following conditions:

Nature of Water	pH	CO_2 p.p.m.	CO_3 p.p.m.	SO_4 p.p.m.	Ca & Mg p.p.m.	Al p.p.m.	Total Solids p.p.m.	Vol. Mat. p.p.m.	Fe p.p.m.	Cl p.p.m.
Polluted......	7.5	4	219	Tr.	180	00	240	160	Tr.	91
Polluted......	7.4	8	102	00	70	Tr.	110	80	00	Tr.
Polluted......	8.0		297		130	00	00	240	180	40
Clean........	7.3		72		Tr.	Tr.	680	640	00	00
Clean........	7.5		135		Tr.	Tr.	520	420	00	Tr.
Clean........	7.5		39		80	00	250	280	00	00

The high pH values here might indicate tolerance for alkalinity, but equally large numbers of this species have been encountered in the clean but acid waters from a cedar swamp. Two hundred and seventy thousand (270,000) *Euglena mutabilis* per cc. have been found in polluted waters at a pH of 2.9 and with ferrous iron as high as 850 p.p.m., but large numbers of the same form also occurred in clean water at a pH of 7.3 and with but a trace of iron present. If we compare the chemical environments of these two Euglenas with that of *Euglena oxyuris* as shown by Senior-White (1928), it becomes apparent why conclusions cannot be based on genera but must be applied to species. He found Euglenids "mainly *E. oxyuris*" present in large numbers only in the absence of free CO_2, i.e. at a pH greater than 8.4. The pool under investigation was a foul one, high in ammonia and phosphates. These species and the two species of Trachelomonas referred to in Table 2 clearly show that little can be judged of the state of the water by their presence. Not only do they fail to indicate purity or pollution, but fail to indicate the presence or absence of iron, although Euglenidae are generally believed to show a preference for iron-containing waters.

On the other hand, *Euglena acus*, *Euglena agilis*, and *Euglena gracilis* may well serve as indicators of heavy organic pollution, for all three thrive where putrescible compounds, such as are found in sewage or in decaying plant infusions, are abundant. But it is only when they are colorless that they indicate such conditions; they apparently do not lose their chlorophyll in relatively clean waters, and specimens brought in from the field are usually green. Those from sewage treatment plants, however, are usually colorless, and when *Euglena acus* is inoculated into a strong hay infusion, it may reproduce rapidly with no vestige of chlorophyll. Only a few chlorophyll bearing flagellates are peculiar to excessively polluted waters. While several commonly occurring green flagellates are often referred to as characteristic of septic or polluted waters, it is their numbers which are significant more than their presence. *Euglena viridis* is so classified (vide Whipple), but according to Table 1 it occurred in about 44 per cent of the clean water samples.

In 1925, seventy-seven samples were taken from unpolluted pools, beginning March 16 and ending October 16. The pH was taken for each sample, and determinations made of CO_2, CO_3, Cl, and SO_4. The following list of species occurred in sufficient numbers to be listed as oligosaprobic forms:

Actinophrys sol	In 4 samples
Clathrulina elegans	In 2 samples
Englypha alveolata	In 4 samples
Trinema lineare	In 3 samples
Chilomonas paramecium	In 6 samples
Entosiphon sulcatus	In 4 samples
Euglena acus	In 4 samples
Menoidium incurvum	In 5 samples
Peranema trichophorum	In 6 samples
Rhipidodendron splendidum	In 5 samples
Synura uvella	In 7 samples
Trachelomonas hispida	In 17 samples
Coleps hirtus	In 3 samples
Cyclidium glaucoma	In 5 samples
Halteria grandinella	In 6 samples
Microthorax sulcatus	In 4 samples

Now these species of Chilomonas, Entosiphon, Menoidium, Peranema, Coleps, Cyclidium, and Microthorax also occur in sufficient numbers in the sludge chambers of sewage disposal plants where decomposition of organic matter is taking place, to be classified as pollution forms. If, however, we look for them in Column 5 of Table 1, it is seen that their occurrence, excepting Cyclidium in sewage polluted streams, is rare. As a matter of fact, at least three considerations must be borne in mind when accepting a protozoan species as an indicator of pollution, viz.: (1) Has it been found to occur frequently in waters known to be polluted, and rarely elsewhere? (2) Does it occur in large numbers in polluted waters, but sparsely elsewhere? (3) Does it thrive in oxygen depleted waters, or only in well aerated waters?

A few organisms readily fall into the first category above, as *Anthophysa vegetans,* or *Carchesium lachmanni,* which are practically never found elsewhere in the field. Still others fall into the second group as *Euglena viridis,* or *Paramecium caudatum.* And the third group includes forms such as *Trepomonas agilis.*

Wherever a genus is referred to an ecological classification, it must be accepted with caution, especially if the genus contains a number of sharply defined species, a condition well illustrated by some of the green flagellates. The Euglenas and allied forms are taken by Marsson (1909) as indicating a foul condition if abundant in pools, an idea I believe to be generally accepted yet far from accurate; the most abundant blooms of Euglenas I have ever seen have been those of *E. polymorpha* and *E. sanguinea,* the one on woodland and swampland pools far removed from sewage or other contamination, the other especially characteristic of open shallow ponds, especially those containing colloidal silt as freshly dug burrow pits alongside roads under construction. They occur elsewhere also, but occurrences as blooms in situations such as the above I would certainly regard as most characteristic.

Euglena viridis, classified as a polysaprobic or septic organism, occurred in 44 per cent of the clear water samples of Table 1, Column 1, and it is not the most common Euglena in the polluted Ohio at Cincinnati as far as present records indicate.

Actually this phase of study of the biology of polluted waters has not been investigated with sufficient exactness. A careful, specific, quantitative and qualitative comparison of clean and polluted waters with an evaluation of attendant environmental characteristics is still badly needed, and will yield very valuable information to the sanitary engineer or worker in water supplies.

SUMMARY

1. Examination of a large number of samples from a variety of habitats has shown that while protozoan species may be cosmopolitan in their distribution, nevertheless a given habitat may be prohibitive to many species because of local environmental characteristics. This is indicated by the continuance of certain species in a given locus, and the failure of other species to occur therein except sporadically.

2. Some few species are shown to occur in such a variety of habitats that they may be regarded as truly cosmopolitan.

3. Seasonal factors as temperature and light seem to affect numbers present, but few if any, species.

4. A wide range of hydrogen ion concentration and chemical composition in natural waters is shown to be tolerated by a number of species.

5. It is probable that in nature food is only a quantitative limiting factor, except for a few species whose food requirements are highly specific.

6. The various types of sewage disposal plants seem to have definite protozoan populations characterized by a large number of species in trickling filters, a much smaller number in activated sludge chambers and the smallest number in Imhoff and septic tanks.

7. Polluted streams *per se* have highly characteristic protozoan populations, but to date no critical evaluation of such a population has been given, and some erroneous generalizations have been made.

8. Protozoa should not be classified ecologically until their range of tolerance of environmental conditions is known.

9. Most species live within such a wide range of tolerance that they are valueless as indicator organisms.

10. A few species are known to be valuable indicators and the number of such species can probably be materially increased.

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FREEZING WEATHER IN RELATION TO PLANT DISTRIBUTION IN THE SONORAN DESERT

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FREEZING WEATHER IN RELATION TO PLANT DISTRIBUTION IN THE SONORAN DESERT

INTRODUCTION

A cold wave of unusual intensity and duration invaded the Sonoran Desert in January, 1937, inflicting considerable frost damage to native plants. Temperatures were generally colder than had been experienced in 24 years, and the reaction of plants afforded evidence concerning the role of winter freezing in determining the geographical distribution of many species. Although a veritable constellation of factors is actually operative in determining distribution, a single factor may occasionally be of predominant importance. The general attitude of plant geographers to this problem has recently been summarized by Mason (1936).

Both the intensity and duration of cold are significant, and the use of minimum temperature figures alone affords a poor index of cold severity. Mean figures of low temperatures are of limited value also, as a single very cold night of a quarter of a century may do more damage to the native species than do all the moderately cold nights combined.

The amount of damage suffered by a plant is influenced by the condition of the plant at the time of freezing—whether the plant is active or dormant, turgid or dry, hardened or not, and mature or young. Certain individuals of a species are inherently more frost resistant than others. The accessory physical conditions play a modifying role—particularly soil moisture, wind, atmospheric humidity, and insolation. Frost damage to plant parts is not a sure index that the entire plant is nearing the limit of its cold endurance.

The Sonoran Desert as a geographical region has been defined by Shreve in a series of papers (see bibliography) in which he has described the distribution of many characteristic species. This natural area embraces most of the Mexican state of Sonora, southwestern Arizona, a small area in southeastern California, and most of the state of Baja California. The flora and vegetation characteristic of this region have been used as a basis in drawing the boundaries, which are shown by the dotted line of figure 1. The Sonoran Desert is not confined, therefore, to the state of Sonora, and is not to be confused with the terms "upper and lower Sonoran life zones."

In this paper we are presenting a summary and discussion of freezing weather[1] in the Sonoran Desert with especial emphasis on the January, 1937, cold wave and its damage to plants.

[1] The specific meaning of the terms "freezing weather" and "frost" are somewhat in doubt "Frost" is sometimes used to refer to the formation of ice crystals on objects during clear, calm, so-called radiation nights regardless of the thermometer reading in a shelter 5 feet above the ground. "Frost" and "freeze" both may refer to a thermometer reading of 32°F. or lower in the 5-foot shelter on radiation nights regardless of the presence or absence of ice crystals on objects. "Frost" and "freeze" are both commonly used to refer to temperature below 32°F. produced by cold waves rather than by radiational cooling. Here "freeze" is used to refer to 32° or lower minimum thermometer readings in the 5-foot shelter, and "frost" to mean the presence of ice crystals.

The authors wish to thank the many observers who have contributed information either of temperature conditions or of frost damage to plants at remote localities. These include Dr. Forrest Shreve, Mr. Jack Whitehead, Dr. I. L. Wiggins, Mr. H. S. Gentry, Dr. R. R. Humphrey, Mr. R. B. O'Neill, Dr. W. P. Cottam, Mr. Fred Gibson, Dr. T. D. Mallery, the Richardson Construction Co., Señor Ernesto Forgach, Mr. James Harding, Mr. L. L. Logan, Mr. Dean Blake, Phoenix Office of the U. S. Weather Bureau, Mr. Aguirre, Mr. L. D. Hoff, the Ferrocarril Sud Pacifico de Mexico, Señor Guillermo Munro, and Mr. Floyd Young.

SYNOPTIC ASPECT OF 1937 COLD WAVE

The following excerpt is from a letter by Dean Blake, Associate Meteorologist, U. S. Weather Bureau, San Diego, California, in which he has described the salient meteorological features of the January, 1937, cold wave:

"Disastrous freezes, that occasionally occur over the southwestern United States, invariably are the result of an abnormal southerly movement of polar air, and the cold wave that overspread the Far West during the latter part of January, 1937 was no exception.

During practically all of January, the polar front which ordinarily lies transverse to our coast line, was nearly parallel to it, conforming in this respect to the axis of the North Pacific high pressure area, which lay northwest to southeast most of the time. Hence, the frontal systems that formed or regenerated over the upper Gulf of Alaska, took a southerly course, each one bringing in its wake Polar Continental (*Pc*) air, which we are forced to conclude from the pilot balloon soundings over the region, came across the mountain ranges of Alaska and British Columbia—an extremely abnormal movement. As these disturbances moved southward they became the medium for the transport of air from the Polar Basin over our western states, giving them a distinctly continental rather than oceanic type of weather.

The outburst of January 18th resulted in the now historic cold wave. A *Pc* air mass with exceptionally low surface temperatures followed closely in the rear of a small depression, which, after its formation in the Gulf of Alaska, passed rapidly southward down the coast of British Columbia, and appeared over our Pacific Northwest on the 19th; Nevada and northern California on the 20th; and southern California and Arizona on the night of the 21st. Most of the Pacific and Plateau States at some time were under its domination, and minimum temperatures lower or closely approaching the record minimum were recorded at most of the stations in these districts."

MINIMUM TEMPERATURES IN THE DESERT

Figure 1 shows the minimum temperatures recorded in and near the Sonoran Desert during January, 1937. Very low temperatures occurred outside the desert on the high plateau of northern Arizona, —29°F. at Pinedale being the coldest. From the northern section of the State there is a drop in altitude in general to the desert, where minimum temperatures ranged

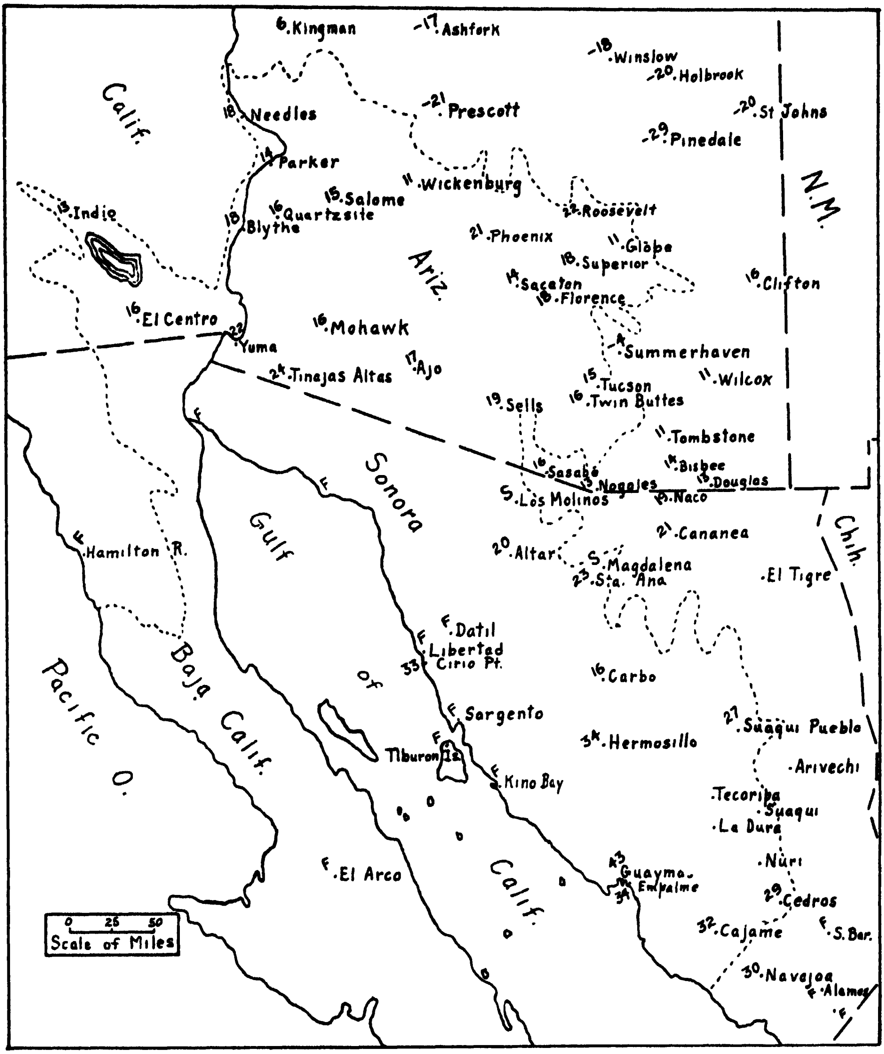

FIG. 1. Sonoran Desert Minimum Temperatures during cold wave of January, 1937. Temperatures are in degrees Fahrenheit, frost data alone denoted by *F*, dotted line represents Sonoran Desert Boundary, S denotes southern limit of snowfall in desert.

from 10 to 20°F. Such a marked difference in minimum temperatures between the two sections of Arizona cannot be explained on the basis of altitudinal considerations alone. Of course, the front portion of an invading cold air mass may be warmed sufficiently in its passage over the land to account for part of the discrepancy, only the front portion reaching the desert and the interior portion of the mass arriving in northern Arizona as cold air overlying an already cooled land surface. Furthermore, the moun-

tain chain separating the plateau of northern Arizona from the desert doubtless acts as a barrier which prevents the lowest, and potentially coldest, air from reaching the desert.

The fact that the desert stations are located quite at random with respect to topography prevents very detailed comparisons of these. However, the coldest desert temperatures occurred in the Arizona section near the northeast border of the Sonoran Desert. One very low reading in southern Arizona was —4° at Summerhaven, a mountain station at an elevation of 7,650 feet, actually above the desert in a coniferous forest. East of the Sonoran Desert the stations at Clifton, Willcox, Tombstone, Bisbee, Douglas, Nogales, Naco, and Cananea are at somewhat higher elevations than the desert stations, but their minimum readings were not appreciably colder. Stations in the state of Sonora did not experience weather as cold as those in Arizona, some actually having no frost. Along the coast of the Gulf of California frost was reported from several localities as far south as Kino Bay, but these were mild, as the 33° minimum at Cirio Point attests.

Light frost was reported at several localities in southern Sonora, the temperature falling to 30° at Navojoa. No frost has been reported from Sinaloa. In Baja California, Hamilton Ranch and El Arco Mine reported light frost.

Figure 2 is a minimum temperature map of the cold wave of January, 1913, the only cold spell on record more severe than the one of 1937. Arizona records only are presented here. In general, the desert stations reported temperatures several degrees colder in 1913 than in 1937. On the other hand the northern Arizona stations experienced colder weather in 1937, but unfortunately, too few stations are involved to lay much stress on these differences. A point of significance also is the fact that the 1937 cold wave lingered over an entire week while that of 1913 passed in three days.

Since ground inversions, which will be discussed later, were more strongly developed in 1913 (table 1), and since most of the stations are influenced by ground inversions, the general severity of the 1913 cold wave may not have been as pronounced as figure 2 indicates. It is highly probable, nevertheless, that the cold waves of 1913 and 1937 were very nearly the most severe ones that have been experienced by the flora of the Sonoran Desert as it is now constituted.

GROUND INVERSIONS

The Desert Laboratory stations are located on and near Tumamoc Hill, which rises 700 feet above the flood plain of the Santa Cruz River. The "hill" station of tables 1 and 2 is situated on the north slope of Tumamoc Hill, 330 feet above the plain from which the hill gradually rises; the "garden" station is on the level plain about 100 yards from the base of the hill. These two stations are one half mile apart, and are about 5 miles from the Tucson station. The data of tables 1 and 2 have been taken from thermo-

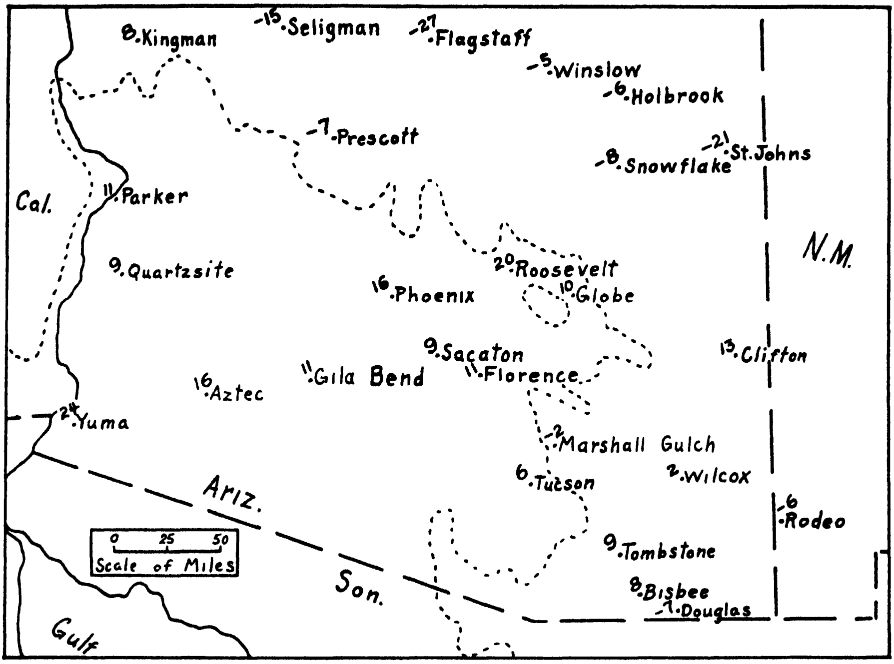

FIG. 2. Sonoran Desert Minimum Temperatures during cold wave of January, 1913. Temperatures are in degrees Fahrenheit, dotted line represents northern boundary of Sonoran Desert.

graph records which were obtained in standard Weather Bureau shelters 5 feet above the ground.

Nocturnal ground inversions of temperature are a common phenomenon in the Sonoran Desert. Young (1921) has studied them in the adjacent region of southern California. A ground inversion is an atmospheric condition in which the temperature increases with elevation from the ground, in basin localities, to as much as 1,000 feet in the air; above this zone a decrease of temperature with elevation exists. The frequence, intensity, and depth of inversions vary with different meteorological and topographic conditions. In earlier literature this phenomenon was called "cold air drainage," a term which infers more than the evidence justifies. These inversions are essentially layers of cold air which lie near the ground on calm, clear nights. They are highly local in character, develop only on nearly cloudless nights, require only a short time to form, are quickly destroyed (as layers with sharp vertical temperature gradients) by moderate wind movement, and vary in numerous details under different conditions of topography.

At the garden station ground inversions are often well developed and nearly of maximum intensity; the hill station is near the top of the inversion layer (Turnage, 1937). These facts explain the relatively low temperatures recorded at the garden station as shown in tables 1 and 2.

TABLE 1. MINIMUM TEMPERATURE DATA FOR "HILL" AND "GARDEN" STATIONS NEAR TUCSON, ARIZONA

Winter	Minumum Temperature		Number of Freezing nights		Number of Freezing hours		Hour-degrees of Temperature below 32 F.	
	Hill	Garden	Hill	Garden	Hill	Garden	Hill	Garden
	Deg. F.	*Deg. F.*						
1912-13	15	1	9		81		480	
1922-23			0		0		0	
1923-24			0		0		0	
1924-25	29		3		18		30	
1925-26			0		0		0	
1926-27	31		1		8		8	
1927-28	31		2		15		15	
1928-29	27		12		43		82	
1929-30	31		1		6		6	
1930-31			0		0		0	
1931-32	20		18		103		367	
1932-33	21	15	8	74	45	394	163	1808
1933-34	28	16	6	45	11	197	24	808
1934-35	21	12	5	36	35	227	130	1349
1935-36	30	19	4	54	5	253	7	1081
1936-37	16	11	15	54	123	336	588	1900

The hill station is perhaps more nearly representative of the general temperature conditions in the largest portion of the desert at elevations between 2,000 and 3,000 feet. The garden station more closely approximates conditions found in the basin areas, canyons and valleys.

Freezing weather in the Sonoran Desert is the result of either the development of a ground inversion at night (which affects only certain areas) or the influx of a cold northern air mass, or both these factors occurring simultaneously. Basins which experience well developed ground inversions are dependent in some measure upon the altitude of the basin; an inversion which would produce a few degrees of frost at Tucson might produce no frost at another basin station 1,000 feet lower under similar conditions.

Although a few inversions do occur which cause the minimum temperature at the garden to be more than 20° lower than that at the hill station, this is seldom the case during the coldest night of winter. The winter minimum usually occurs when a cold air mass has invaded the region as a consequence of the passage of a cyclone. The meteorological conditions of the storm are such as to inhibit the maximum development of an inversion. The minimum temperatures of the 1936-37 winter illustrate the influence of storm conditions at the time of coldest weather when the garden was only 5° colder than the hill station (Fig. 4). The 1912-13 winter minimum occurred on a more calm night, and the difference between the two stations was 14°F.

TABLE 2. GREATEST NUMBER OF CONSECUTIVE HOURS AND OF HOUR-DEGREES BELOW 32° F., DATES OF FIRST AND LAST FREEZES, AND LENGTH OF FREEZE SEASON AT "HILL" AND "GARDEN" STATIONS NEAR TUCSON, ARIZONA

Winter	Greatest number of consecutive hours below 32 F.		Greatest number of consecutive hour-degrees below 32 F.		Dates of first and last freezes		Lergth of freeze season (days)	
	Hill	Garden	Hill	Garden	Hill	Garden	Hill	Garden
1912-13	19		214		Jan. 6 Mar. 31		84	
1922-23	0		0				0	
1923-24	0		0				0	
1924-25	8		17		Jan. 13 Jan. 18		6	
1925-26	0		0				0	
1926-27	8		8		Dec. 28		1	
1927-28	9		9		Feb. 16 Feb. 17		2	
1928-29	11		37		Dec. 11 Feb. 27		78	
1929-30	6		6		Jan. 9		1	
1930-31	0		0				0	
1931-32	15		85		Dec. 15 Feb. 4		51	
1932-33	14	15	90	148	Dec. 26 Feb. 11	Nov. 10 Apr. 20	47	161
1933-34	5	12	14	106	Dec. 17 Jan. 14	Nov. 5 Apr. 4	28	150
1934-35	16	17	95	136	Jan. 20 Mar. 10	Nov. 21 Apr. 10	49	140
1935-36	2	10	3	86	Jan. 2 Jan. 20	Oct. 24 Apr. 6	19	164
1936-37	19	17	185	193	Jan. 3 Feb. 9	Nov. 3 Apr. 24	37	172

The ground inversion is also responsible for considerably more freezing nights in the garden than on the hill. In the winter of 1931-32 there were 18 freezing nights on the hill, but no freezing temperatures were recorded in four of the winters shown in table 2. At the garden there have been from 36 to 74 freezing nights each winter. The garden is also subjected to freezing weather considerably earlier in the fall and later in the spring than is the hill station. During the periods covered by these records—15 consecutive years at the hill and 5 consecutive years at the garden—the earliest freeze at the former station occurred December 11 and at the latter October 24; the latest freeze of spring at the former station occurred March 31 and at the latter April 24. The very early and very late occurrences of frost at the garden extend well into the growing season and exert a deterrent effect on vegetative activity.

The combination of many more freezing nights and of appreciably lower temperatures at the base of the inversion is responsible for the markedly greater number of "hour-degrees" of freezing weather in the garden. This

datum is an attempt to coordinate the influences of intensity and of duration of freezing weather somewhat along the lines suggested by MacDougal (1914). Seasonal totals range from 808 to 1,900 hour-degrees at the garden and from 0 to 588 at the hill. More significant than seasonal totals, as far as frost damage to established plants is concerned, is the number of consecutive hour-degrees of freezing weather. In only one year of five has the greatest number of consecutive hour-degrees fallen below 100 in the garden; only in one year of the last 15 has it risen above 100 on the hill.

The fact that during the one very cold night (January 22, 1937) of nearly a quarter of a century the cold conditions were such that the garden and hill endured approximately the same number of hour-degrees—193 and 185 respectively—appears to be important. The freeze of January 7, 1913, with 214 hour-degrees on the hill, was slightly more severe, and indicates further that occasional freezes above the body of air subject to the development of a ground inversion are as severe as those within an inversion layer. Furthermore, table 1 reveals that the year to year variation in severity, as measured by hour-degrees, is much greater on the hill than in the garden.

A ground inversion freeze which falls to a given minimum temperature produces appreciably fewer hour-degrees than does a purely cold-air-mass freeze. For instance, the coldest night of the 1933-34 winter, a ground inversion phenomenon largely, reached 16° and produced 106 hour-degrees below 32° at the garden. The 16° minimum at the hill in the winter of 1936-37, a cold wave, produced 185 hour-degrees. Although cooling is rapid at the base of the inversion layer after sundown, the general heat conditions of the entire air mass are usually such that the duration of the freeze is limited. In the cases cited the inversion freeze lasted 12 hours while that of the cold wave lasted 19 hours.

ANOTHER THIN INVERSION LAYER

There is another fact of significance concerning inversions which is not shown by the ordinary records. During inversion nights a very thin layer (several inches) of cold air lies next to the ground of hill slopes. This layer is to be distinguished from the main inversion layer in that it is much thinner, has a very steep temperature gradient, is not found at all spots on the slope, and may or may not lie within the larger inversion layer. An alcohol minimum thermometer was exposed openly one inch above the ground at the hill station. The minimum temperature record thus obtained compared very closely with that of the garden thermograph (5 feet above the ground and in a shelter). Numerous checks with thermocouples and mercurial thermometers, variously painted and variously shielded, indicated that the error due to open exposure of the alcohol thermometer was of slight significance as far as the present inference is concerned. Likewise, readings were obtained in the patio of the nearby Laboratory building. These revealed no marked difference between the surface air layer in the patio and the 5-foot layer of the hill temperature station.

Hence there are certain spots on hill slopes where the cold conditions of a thin layer of air are very similar to the conditions of larger layers in the basins. Minimum temperatures, length of the frost season, and number of freezing nights are closely parallel, judging from the meagre data available. This thin layer of cold air on the hill slopes, while of little moment to the larger plants, is a strong force with which all seedlings must contend. There are many spots which, like the Laboratory patio, do not have this thin, cold layer, no doubt, but the authors' experience indicates these to be the exception rather than the rule.

DURATION OF FREEZE OF PARAMOUNT IMPORTANCE

As Shreve (1911, 1914) has demonstrated, the number of consecutive hours of freezing weather is a cold temperature datum of paramount importance in this region. Figure 3, by Shreve, presents isochronals for the longest number of consecutive hours of freezing temperature at selected stations. In the Sonoran Desert there is no record of a single day (between two cold nights) when the air temperature failed to rise above 32°. At Tucson there have been two occasions of 19 consecutive freezing hours (table 2). These occurred on the hill; the longest freeze at the garden was 17 hours. The lowest maximum daytime air temperature record at the hill station was 35°—January 7, 1913—with 15 hour-degrees above freezing and 6 hours above freezing during the day, preceded by 19 hours and followed by 15 hours below freezing. The second lowest maximum, 36°, occurred January 22, 1937; there were only 5 hour-degrees above freezing and 2 hours

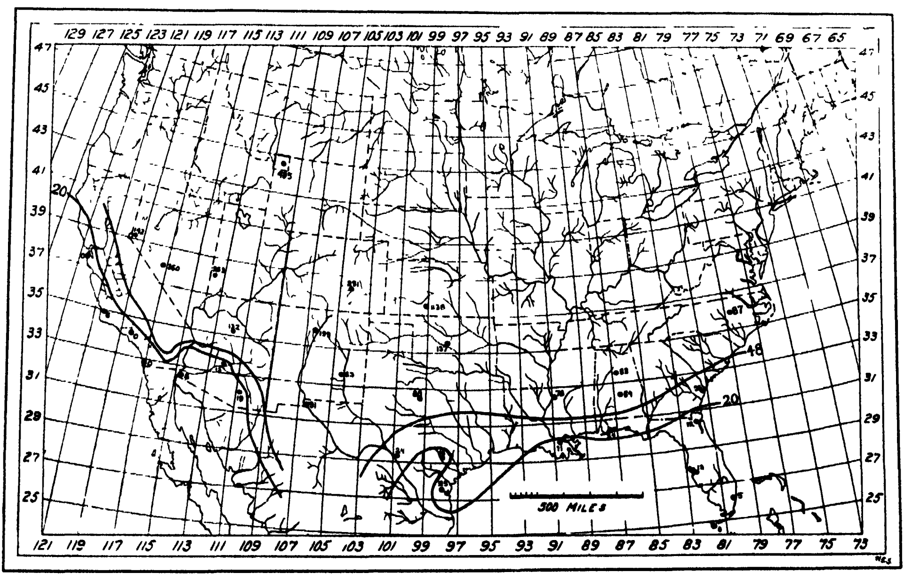

FIG. 3. Isochronals for longest number of consecutive hours of freezing temperature, 1917-20. (After Shreve.)

above freezing during the day, also preceded by 19 hours and followed by 15 hours below freezing.

This short duration of freeze contrasts sharply with that found in northern Arizona where there are often 5 consecutive days and nights of continuously freezing air temperatures. Although minimum temperatures are very little lower in the region east of the Sonoran Desert than are the desert temperatures, as figures 1 and 2 show, the duration of freezing weather is probably considerably longer. This is evidenced by the Bisbee record of January 7, 1913, when the maximum daytime air temperature failed to rise above 24°. The freezing weather at Bisbee on that date lasted at least 36 consecutive hours or nearly double the duration of Sonoran Desert freezes. The higher mountain peaks in, or rather above, the desert also have freezing weather which extends over a period of several days and nights, as shown by the Santa Catalina record to be discussed later.

Figure 4 shows thermograph traces of the January, 1937, cold wave which invaded the region as a cyclonic storm; the broken line is the hill station and the unbroken line is the garden station record. During the first two nights, with storm conditions prevalent, no inversion developed. The third night, January 22, which was the coldest night, only a slight inversion developed. The following nights, after the storm center had passed, inversions were somewhat more pronounced, but the air mass was not as cold as in the earlier stages. The record for March 2, 1937 (Fig. 4) illustrates the nature of the temperature curves when an inversion is fairly well developed. It further illustrates the occurrence of freezing weather in the garden on nights when the air mass is in general fairly warm and temperatures at the hill station are mild.

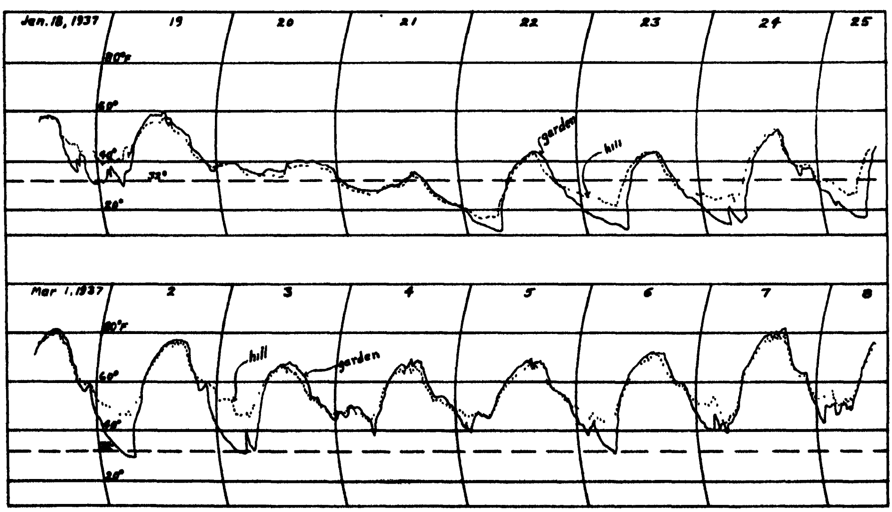

FIG. 4. Thermograph records from garden and hill stations, Desert Laboratory, for the January, 1937, cold spell and for week ending March 8, 1937, a typical winter season week.

The temperature of the soil is also a datum of some value in this connection. The only instrument from which we have a soil temperature record is a Freiz soil thermograph with bulb buried as shallowly as possible in the adobe soil of the garden station. The maximum soil temperature of January 21, 1937, was 41°F. followed by a minimum of 18°. For 18 consecutive hours the temperature was below 32° and there were 161 hour-degrees below 32°. During the next 3 days and nights the soil was only slightly warmer, fluctuating diurnally between about 50° and 20°. This soil, quite moist, froze to a depth of 3 inches. Rains and snows earlier in the month, amounting to 1.50 inches of precipitation, had left the first 10 inches of soil very moist. In shady spots on the north slope of Tumamoc Hill snow remained on the ground for one week, although in most places it had melted after a few hours of sunshine.

Wind velocities at Tucson during the snow storm preceding the coldest weather were rather high, approximately 10 miles per hour. During the coldest period the air was relatively calm, from 3 to 7 miles per hour.

MOUNTAINS OVERLOOKING THE DESERT

The pine-clad Santa Catalina Mountains stand on the eastern edge of the Sonoran Desert, a few miles north of Tucson, and rise to an elevation of 9,150 feet. Minimum temperature readings at several stations on the Santa Catalina slopes were reported by Shreve (1914) for the winter of 1912-13. During that severe winter the garden station, at the base of an inversion, recorded 1°; the coldest reading, —6°, occurred at an altitude of 6,000 feet on a ridge; in a canyon at 7,700 feet the minimum temperature was —2°.

Daily readings were made by Mr. R. B. O'Neill throughout the 1933-34 winter at Summerhaven, altitude 7,600 feet, in a canyon of the Santa Catalinas. This was a rather mild winter and the coldest temperature at Summerhaven was 17° as compared with 16° at the garden and 28° at the hill station. Again daily readings were made at Summerhaven throughout the severe 1936-37 winter. The minimum at Summerhaven of —4° compares with 11° at the garden and 16° at the hill.

These data indicate that the high mountains of southern Arizona do not experience minimum temperatures very much colder than are those of the desert lowlands, and not nearly as cold as stations at comparable elevations on the plateau of northern Arizona.

The Summerhaven station from November 25, 1933, until the summer of 1934 had 57 nights of temperature below 32°. The garden station over the same period had 39; the hill had only 6 nights. From December 7, 1936, until the summer of 1937 the Summerhaven station experienced 103 nights below 32°, the garden 51, and the hill 15 nights. The last 32° minimum of the 1934 spring occurred at Summerhaven April 7, at the garden April 4, and at the hill January 14. In 1937 the last 32° minimum of spring occurred at Summerhaven May 1, at the garden April 24, and at the hill February 9.

It has long been suspected that the most potent cold temperature factor on the high mountain slopes of southern Arizona, in so far as the absence of desert plants is concerned, is the duration of the freezing spells. Mr. O'Neill's Summerhaven records lend considerable weight to this hypothesis. In the 1933-34 winter there were two consecutive days in which the maximum temperature reached only 28° and 30° respectively, during a prolonged snow storm. The duration of that freeze was about 60 hours. There were two other occasions when single days were without thaw. One of these experienced snow; the other came several days after a storm.

The January, 1937, cold wave produced maximum temperatures at Summerhaven of 32°, 26°, 22°, 32°, and 26° for 5 consecutive days. This was a period of about 130 consecutive hours without thaw, which is closely comparable to freeze durations in northern Arizona. Earlier in the winter there was a period of 4 consecutive days without thaw, another of 3; later there were periods of 1 day and of 2 days. All of these periods except the one of a single day occurred in conjunction with snow storms.

There is a need for thermograph records from stations on the desert boundary in order to determine more accurately the cold temperature features which correlate with the change in vegetation. The northward and vertical limits of desert vegetation in Arizona appear to be determined by the fact that the duration of occasional freezes beyond these boundaries amounts to from 36 to 130 hours, but further detailed evidence is needed.

YAQUI RIVER RECORDS

In table 3 are given the annual minimum temperature records of the periods 1927 through 1930 and 1933 through 1936 from several stations on the Yaqui River of Sonora and Chihuahua. These data were kindly supplied by the Richardson Construction Company of Cajeme, Sonora. Figure 1 shows the location of several of the stations. Madera and Dolores are just off the map in Chihuahua east of Arivechi. At the desert stations of Suaqui, La Dura, Tecoripa, San Xavier, and Nuri only two occasions of mild freeze were noted for the periods covered. At Arivechi and Dolores,

TABLE 3. MINIMUM TEMPERATURES ALONG THE RIO YAQUI[1]

		Elevation	1927	1928	1929	1930	1933	1934	1935	1936
La Dura,	Son....	500 ft.	49°F.	43.0	46.5	44.5	46.5	35.5	41.0	37.6
Nuri,	" .	1,000	48.0	46.5	35.5	48.0	44.5	35.5	35.5	34.0
Tecoripa,	" . .	1,000	39.0	32.0	34.0	39.0	41.0	37.5	32.0	35.5
Arivechi,	" .	2,000	14.0?	12.0?	14.0?	12.0?	35.6	30.0	26.5	34.0
Suaqui,	" . .	1,300	41.0	37.5	39.0	39.0	43.0	32.0	17.5?	35.5
San Xavier,	"	. . . .	43.0	41.0	39.0	39.0	46.5	43.0	41.0	41.0
El Tigre,	" . . .	4,000	28.5	21.0	25.0	25.0	19.5	30.0	17.5	28.5
Dolores,	Chih.	3,700	34.0	32.0	32.0	5.0?	34.0	34.0	32.0	34.0
Madera,	" . . .	7,000	12.0	10.5	8.5	7.0	16.0	16.0	17.5	16.0

[1] A question mark (?) is placed after the readings which appear to be in error with respect to a comparison of the mean monthly minimum records for these stations for the different years.

just east of the southern part of the Sonoran Desert, freezes are more common but also mild. El Tigre is visited by cold every year, and probably has a weather regime similar to that at Douglas and Bisbee. Madera, high in the heart of the Sierra Madre, is visited by freezes every year, the lowest minimum noted in these data being 7°. In the Sierra Madre the duration of freeze is not known from available records. It is possible that the eastern edge of the desert, against the slopes of the Sierra Madre, is determined by factors other than cold weather.

INFLUENCE EXERTED ON VEGETATION BY COLD WAVE OF JANUARY, 1937

The desert merges gradually into thorn forest in southern Sonora. In this transition region there is a profound change in plant life (Shreve, 1934) which correlates with the southern extension of freezing weather (excepting in the mountain areas). Undoubtedly many of the species of the south are unable to endure frost, although there are probably many other species for which frost is not a critical condition in checking their northward extension. Distributional evidence indicates that the thorn forest has contributed heavily to the Sonoran desert flora, and the inference is strong that this contribution is still going on—that many species here will continue to migrate slowly northward.

The data on frost damage are presented in geographical order beginning with the southern edge of the desert and working northward.

Southern Sonora

Our sincere thanks are due Mr. Howard Scott Gentry for the full use of his notes on the plants of southern Sonora. The coldest temperature recorded was 29°F. at Cedros with 5 nights of frost.

Among the species injured are:

I. Species with northern limit in southern Sonora

- A. Leaves and branches damaged
    - Ficus, several species, including *F. cotinifolia* and *F. petiolaris*
    - *Pithecolobium dulce*
    - *Randia echinocarpa*
    - *Perityle cordifolia*
    - *Mammillaria* sp. crown damaged in several species
    - *Tournefortia Hartwegiana*
- B. Leaves damaged
    - *Albizzia tomentosa*
    - *Quercus albocincta*
    - *Ichthyomethia mollis*

C. Flowers damaged
Brongniartia lunata

II. Species with northern limit in central Sonora
A. Leaves and branches damaged
Guazuma ulmifolia
Caesalpinia pulcherrima
B. Leaves damaged
Lysiloma Watsoni
Randia obcordata
Jacquinia pungens
Stegnosperma halimifolium
C. Flowers damaged
Ipomoea arborescens

III. Species with northern limit near northern boundary of Sonoran Desert
A. Leaves and branches damaged
Franseria ambrosioides
B. Leaves damaged
Sapindus Saponaria
C. Flowers damaged
Asclepias subulata

Cultivated plants damaged and in some cases killed in southern Sonora include *Citrus spinosissima, Carica papaya, Musa sapientum,* and *Ricinus communis.*

Pentstemon Parryi, which has its southern limit in this region, suffered frosted flowers.

SASABE TO ALTAR AND TIBURON ISLAND

Late in April, 1937, one of the authors journeyed from Tucson to Tiburon Island via Sasabe, Altar, Datil, Libertad, and Sargento. Although frost damage was more difficult to discern at that late date, some damage was nevertheless apparent. Figure 1 shows the minimum temperatures along this route.

Leaves and twigs of *Celtis pallida* and *Olneya Tesota* were injured as far south as the vicinity of Datil. Tips of branches of *Lophocereus Schottii* were frosted on occasional plants in some localities from Altar to Datil. Leaves and shoots of *Bursera microphylla* were damaged at every locality excepting the interior of Tiburon Island, and the leaves were killed on plants near the Cirio Point station, where the minimum temperature was only 33°. No damage was noted on *Pachycereus Pringlei.* Judging from the appearance of the plants, the Datil area had received more cold weather than any other locality south of the border along this route.

PAPAGO RESERVATION

The authors owe their thanks to Dr. R. R. Humphrey, who spent the 1936-37 winter on the Papago Reservation between Sells and Ajo, for the use of his observations on frost damage. Here leaves and stems were damaged on *Olneya Tesota*, *Bursera microphylla*, *Jatropha cardiophylla*, *Encelia farinosa*, and *Sapium biloculare*. Tips of *Lemaireocereus Thurberi* were injured.

Just south of Ajo is the northern limit of *L. Thurberi* excepting the occurrence of a single large individual on a slope of the Picacho Mountains about 40 miles northwest of Tucson. This unique individual was not damaged by the cold weather, due partly to its location with respect to surrounding topography where it escapes the nocturnal inversions of temperature. Although the tips of the plants near Ajo were killed, growth has resumed without the loss of many if any individuals.

TUCSON REGION

Among the native species leaves and twigs of *Olneya Tesota* and *Celtis pallida* were killed. In many cases stems were killed to the ground in *Franseria ambrosioides*, *Jatropha cardiophylla*, and *Encelia farinosa*. Frosted leaves were noted on *Dodonaea viscosa* growing in the arroyo bottoms.

Several individuals of *Lophocereus Schottii*, *Lemaireocereus Thurberi*, and *Rathbunia alamosensis*, which had been imported from Sonora several years ago and planted at the Desert Laboratory, suffered dead tips, but all these plants have resumed growth. *Ceiba acuminata*, imported from Sonora, suffered death to stems at Tucson but later sent up new shoots. Seedlings of *Zizyphus sonorensis* and *Pithecolobium sonorae* were killed at the Desert Laboratory Garden. One young *Jatropha cordata* was killed, another has recovered.

Of the Opuntias no record was kept concerning frost damage. Exotic plants in the Laboratory greenhouse, as well as native seedlings, were unhurt, as the greenhouse had been heated in anticipation of the cold wave. Palm and citrus trees around Tucson suffered varying degrees of injury. Old leaves of *Prosopis velutina* Wooton were shed during the cold spell, but this may have been due largely to the snowfall. Leaves of *Cercidium Torreyanum* and *C. microphyllum* were killed. *Idria columnaris*, from Sonora, was not injured at Tucson.

In January *Fouquieria splendens* was not in leaf. However, the young leaves of one individual at the garden were killed by the frost of February 21, 1937. This inversion type of cold weather produced 8 hours of frost, 58 hour-degrees below 32°, and a minimum temperature of 21°. A month later new leaves had come out again on this individual.

SUPERIOR REGION

Mr. Jack Whitehead, to whom the authors are deeply indebted for his contribution, observed the frost damage to native species in the vicinity of

Superior, and also listed the damage done to the many exotic plants of the Boyce Thompson Arboretum.[2] The cold conditions at Superior were comparable to those at Tucson, the minimum temperature being somewhat higher, however (see figure 1).

Around Superior damage to leaves and stems was suffered by *Olneya Tesota, Celtis pallida, Asclepias subulata, Encelia farinosa, Dodonaea viscosa,* and *Simmondsia californica.* The last two species were in flower at the time of the freeze, the flowers being killed. As a result the 1937 seed crop of *S. californica* was extremely meagre. Frost damage to all these plants was variable from one locality to another, some stands of *Olneya Tesota* and *Dodonaea viscosa* showing little or no injury. *Franseria ambrosioides* stems were killed to the ground. With the advent of the growing season all these species resumed growth.

Among the species cultivated in the Arboretum grounds *Lysiloma Thornberi,* native to the Rincon Mountains near Tucson, suffered considerable damage but recovered. Among plants more or less severely injured were: *Randia Thurberi, Duranta Plumieri, Karwinskia Humboldtiana, Lantana Camara, Tecoma stans,* and *Fouquieria peninsularis,* all of which are native to the southern portion of the Sonoran Desert in Sonora or Baja California.

Some damage to cacti—*Lemaireocereus Thurberi, Opuntia Bigelovii, Opuntia fulgida mammillata,* and *Opuntia leptocaulis*—occurred at the Arboretum. Cacti badly damaged included *Lophocereus Schottii, Pachycereus Pringlei, Rathbunia alamosensis, Mammillaria microcarpa* and *M. Milleri.* The last two showed death of many individuals, which is surprising in view of the fact that the range of these species is roughly from Kingman to Phoenix near the northern boundary of the desert.

NORTHERN PART OF SONORAN DESERT

After the cold wave Dr. Shreve noted dead twigs and foliage of *Olneya Tesota* at its northern limit immediately north of the Bill Williams River; the same condition prevailed in the *Olneya* region of southern California. *Franseria ambrosioides* throughout the Bill Williams Valley at its northern limit was killed to the ground. Leaves and branches of *Eucnide urens* were frost damaged. *Encelia farinosa* growing in the lower spots of the Bill Williams region was damaged, but little injury was observed to those plants growing somewhat higher on the slopes, presumably above a ground temperature inversion. In the Tucson Mountains at its northernmost locality *Eysenhardtia orthocarpa,* observed in late summer, appeared to have been frosted to the ground, but new shoots were abundant.

SOUTHERN UTAH

In the vicinity of St. George, Utah, several Sonoran desert species reach their northern limit. Cottam (1937) has reported severe damage to *Covillea*

[2] This list of exotic plants which were damaged will be supplied by the authors to any reader who wishes it.

tridentata (*Larrea tridentata*), *Strombocarpa odorata* (*Prosopis pubescens*), and *Prosopis glandulosa*. Dr. Cottam has recently informed us that all these species are recovering, new growth from primary branches being abundant, but that at the higher elevations the mortality to *Larrea* and *Prosopis glandulosa* was as high as 80 per cent of the individuals. The freeze, which was the most severe on the St. George records, produced 7 consecutive days of weather below 32° and a minimum temperature of —11°.

BAJA CALIFORNIA

From Baja California we are informed by Mr. L. L. Logan that occasional banana trees were injured at Hamilton ranch. Mr. James Harding reports frost damaged leaves to "torote" (probably *Pachycormus discolor*).

DISCUSSION

The cold wave of January, 1937, was in many respects the most severe freeze that has invaded the Sonoran Desert during the period covered by climatic records. The influence of this freeze on the various species of plants affords some indication of the role of freezing weather in determining the distribution of the desert flora. Conclusions, however, owing to the complexity of this problem must be drawn with care.

The entire area of the Sonoran Desert is subject to occasional frosts. The low country bordering the Gulf of California, southern Sonora, and the desert of Baja California experience less cold weather than do other parts of the desert. The coldest weather is experienced by the northern fringe of the desert in Arizona and by the plains at higher altitudes.

Topographic location contributes to extreme variability in the incidence of freezing weather, stations situated within the ground inversion zone receiving considerably more cold air than others. However, occasional cold waves, often occurring only once in several years, produce the extreme freezes at all stations, and cause the most damage to plants

Two features of cold temperature stand out above others. The first is the occurrence of frost; the second is the duration of freezing temperatures throughout a night, the following day and the following night, and even longer perhaps. The southward limit of this first cold weather datum coincides roughly with the northward extension of the tropical thorn forest (southern limit of the desert). The second datum coincides with the northern limit of the Sonoran Desert and with the vertical limit of desert vegetation on mountain slopes and tablelands. Although the most profound changes in vegetation occur at these boundaries, there are many species which have their distributional limits somewhere between them.

For certain of the latter group of species, no doubt, there are intermediate cold temperature features made up of both intensity and duration which are critical. We do not yet have definite evidence as to the quantities.

A few species extend beyond the Sonoran Desert. *Larrea tridentata* has endured at St. George, Utah, a period colder than any occurring on the high mountain slopes within and bordering the desert, on which this species is not found. *Fouquieria splendens* grows beyond the desert in regions where the duration of a freeze is more than 36 hours.

The northwestern boundary of the Sonoran Desert in California, where the Sonoran and Mohave Deserts meet, does not correlate with the cold temperature features we have discussed. The absence of characteristic Sonoran species in the Mohave Desert is thought to be related to the absence of summer rainfall.

With the exceptions of *Prosopis glandulosa* and *Larrea tridentata* at some localities near St. George, Utah, we have no evidence that wholesale killing of any species has occurred along its northern, or cold, limit. The fact that injury to *Franseria ambrosioides*, for instance, was almost as severe in southern Sonora as in the Bill Williams region indicates that partial killing of a plant is not an infallible index that the critical cold temperature has been approached.

Nevertheless, it is highly probable that those species which experienced damage are hindered by cold weather from migrating much farther into colder regions. Among these species, which extend to the northern boundary of the desert, are *Olneya Tesota, Franseria ambrosioides, Encelia farinosa, Simmondsia californica, Celtis pallida, Mammillaria microcarpa*, and *M. Milleri.*

Although no damage to *Carnegiea gigantea* was noted, it has probably migrated as far north as cold weather will allow (Shreve 1911). In fact, in the 1913 cold wave Thornber (1916) reported death to young Carnegieas growing near their altitudinal limits. There are many species, no doubt, which suffered no damage in the recent freeze but are unable to endure the long duration of cold weather characteristic of the region north of the desert.

Among the species which have their northern limit near a line between Yuma and Superior those which were frost damaged include *Bursera microphylla, Lemaireocereus Thurberi, Dodonaea viscosa, Asclepias subulata, Sapium biloculare, Jatropha cardiophylla, Lysiloma Thornberi*, and *Eysenhardtia orthocarpa*. The Desert Laboratory record of a minimum temperature of 16°F., 19 consecutive hours of freezing weather, and 185 consecutive hour-degrees below 32° is some index of the critical cold for these species. A minimum temperature near 0°F., 20 consecutive hours and about 250 hour-degrees below 32° is probably a fair index of the critical cold endured by the species which suffered along the northern border of the desert.

Among the Sonoran Desert species which do not extend into Arizona those which suffered frost injury at Superior or Tucson (in cultivation) included *Pachycereus Pringlei, Lophocereus Schottii, Rathbunia alamosensis,*

seedlings of *Zizyphus sonorensis* and *Pithecolobium dulce, Jatropha cordata, Randia Thurberi, Duranta Plumieri, Karwinskia Humboldtiana, Lantana Camara, Fouquieria peninsularis*, and *Tecoma stans*. Few of these, however, were completely killed.

Mild frost in Baja California damaged *Pachycormus discolor*. The injured plants of southern Sonora, where frost was not extreme, have already been listed in the order of their distributional limits. Several of these species, although injured by mild frost in southern Sonora, extend into the central part of the state where freezes were somewhat more severe.

Of considerable interest is *Idria columnaris*, which was unhurt by Tucson's freeze, although its native habitat is in the relatively mild regions to the south.

Since our information concerning the various aspects of cold weather is limited at the present time, an imperfect picture of frost conditions in the Sonoran Desert is presented. The thin layer of cold air near the ground, presumably at most topographic sites on inversion nights, is probably a potent factor in a seedling's struggle for establishment. We know very little as yet about this air layer. Also, available temperature records seldom reveal information concerning duration of frost. Very few records exist of soil temperatures and the duration and depth of soil freeze. Most observers are still content with a record of daily maximum and minimum air temperatures obtained at an arbitrary height and place and of relatively insignificant "mean" figures. Very few attempts have been made to determine experimentally the critical temperature features for various plants.

Distribution of species under present climatic conditions surely has not reached a static state. Perhaps the northern limit of many Sonoran Desert species might be determined by factors other than winter cold, for instance, moisture relations. Accessory physical conditions might greatly modify the influence of cold weather—to such an extent that a single datum of freeze is a poor index of the limiting factors when applied to different localities and at different times for the same species. These are problems for the future.

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THE RELATIONS OF TEXAS ACRIDIDAE TO PLANTS AND SOILS

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CONTENTS

THE RELATIONS OF TEXAS ACRIDIDAE TO PLANTS AND SOILS

INTRODUCTION[1]

Grasshoppers and war have come down through the ages as an ever-present twin menace to the amplitude of man's bread basket.

Grasshoppers, at least, have proved useful as well as destructive. The accumulation of three decades of significant cytological and genetical researches by McClung, Nabours, their colleagues and students has focussed the attention of biologists on the Acrididae as suitable material for the investigation of fundamental problems of biology. *Melanoplus differentialis* (Thos.) in the laboratories of McClung and Bodine has come to be recognized as a standard laboratory animal (Hodge 1933, p. 306), useful in the study of morphological, physiological, embryological and related problems. Furthermore, in addition to their taxonomic, evolutionary, and economic importance, animal ecologists have been looking to acridians as promising material which may afford some clues as to the relative individual values of the intricate complex of ecological factors which are involved in the interrelationship of terrestrial biota.

THE PROBLEM STATED

What are the factors that influence and control local distribution of the Acrididae? Is local distribution of grasshoppers chiefly correlated with the distribution of host-plants, with the food and protection afforded by the vegetation? How do different kinds of soils, soil texture, soil structure, soil moisture, chemical make-up of soils affect local distribution? To what extent do general climatic conditions, temperature, sunlight, humidity, and evaporation control distribution?

In some instances local distribution takes on the aspect of definite zonation and has been described as zonal distribution. In other areas zones are not apparent and a field study station is best described as a complex of intermingled habitats.

What is the relative importance of these environmental factors? To get an answer or a partial answer to this query has been the focus of a continuous series of field and experimental studies by the writer for the past seven years. Based on these researches, begun with field studies in 1931, an effort is being made in the present paper to analyze especially the plant and soil interrelationships of north central Texas acridians; and further to

[1] During 1935 and 1936 the writer was assisted in these investigations by grants-in-aid from the National Research Council. The 1937 experiments were supported in part by a grant from the Penrose Fund of the American Philosophical Society.

make a contribution to the understanding of the terrestrial biota as it is found in *north central* Texas.[2]

The statement of the Entomological Commission (Riley, Packard, and Thomas 1877, p. 13) applied to the "Rocky Mountain locust," *Melanoplus spretus* Walsh, as "devouring everything green" has been carried over generally by authors in describing the feeding behavior of grasshoppers.

Economic entomologists in describing the feeding activities of grasshoppers as a rule do not discriminate between "pest" species and those species which have not, as yet, been proven harmful to agriculture. The implication always is that all acridian species are potential enemies of cultivated crops. The following citations are typical. Essig (1926, p. 72) describes grasshoppers as "omnivorous feeders"; Herrick (1925, p. 328) as "destroying everything in their path"; Fernald (1921, p. 82) as "feeders on grasses and vegetation in general." Criddle (1933a, p. 478) is more critical in his observations. He points out that even *Camnula pellucida* Sc., a serious grasshopper pest, is a restricted feeder, and in cage tests he has shown that many Manitoba acridians are selective feeders.

Among recent ecological investigators, Wolcott (1936, pp. 79, 81) states that grasshoppers "like cows feed on any kind of vegetation," and Strohecker (1937, p. 245) says that "such plants as can be used for one species are equally useful for others." On the other hand, Ball (1936, p. 680), chiefly on the basis of his field studies, emphasizes "the diversity of adaptation and at the same time the fixity of these food habits."

In a recent paper (Isely 1937, p. 325) I have emphasized the importance of soils in explaining the local distribution of acridians. The further discussion of relations of the Acrididae to soils in the present paper is based in part on experimental data. These were secured by testing acridian reactions in choosing soils of different structure and texture for oviposition. Additional field data based on further critical studies of hatching sites are also discussed.

Experimental testing of acridian plant preferences for food, and soil choices for oviposition, was begun in 1935 and continued during 1936. Recheckings and additional studies were made in 1937.

Topography and vegetation as related to drainage and shelter are important factors of the environment. Preliminary experiments dealing with variation in temperature and humidity correlate with field data in pointing to vegetation-cover for shelter as an important factor which must be further evaluated in explaining local acridian distribution. The habitat factors covering distribution in various micro-habitats as well as eco-climates[3] and microclimates have not been experimentally studied. Only general climatological conditions are, here, taken into account.

[2] In previous papers by the writer (1935, 1937) the acridian species studied came from widely separated stations in northeastern Texas. The experimental species which have supplied the data for this paper belong primarily to a more limited area geographically. Hence, the limitation, *north central Texas.*

[3] The sum-total of meteorological factors within a habitat (Uvarov 1931, p. 128).

In attempting an analysis of certain factors that control local distribution, it may be well to define the scope of the distribution implied. Local distribution as here used means distribution within a limited area, an area which can be given a comprehensive examination in two or three hours' time by an experienced field worker. For a final thorough evaluation of the factors controlling local distribution from the viewpoint of field ecology, the same series of habitats of a given field-station should be examined at least bimonthly so as to make sure of seasonal succession. For an understanding of annual fluctuations several years of continuous study would give more complete data. Diurnal and weather variations should not be overlooked in planning field study trips.

A field station should represent a specific type of habitat. The topography should be essentially uniform and the vegetation-cover similar as to plant species and density of cover. The area should be large enough (ten to twenty acres) to insure permanence of typical species even in unfavorable seasons. Marginal areas should be available for comparison. Possibly a better picture of what I mean by a limited area may be indicated by describing specific areas or local field-stations; for example: a sandy east Texas post oak cross-timbers tract including timber margins; a Houston clay shallow phase, upland, weedy pasture; a Houston black clay, level meadow; an eroded chalk or marl tract of rough, waste-land with sparse cover of mixed vegetation; an alluvial Trinity clay, creek valley, weedy-pasture including stream margins.

These general habitat types are represented at field-stations in Ellis, Dallas, and Johnson counties in north central Texas. These areas have essentially uniform[4] general climatological influences. Such climatological factors have been determined by making use of the United States weather records: temperature, precipitation, pressure, wind, sunshine, and in some instances humidity and evaporation.

LITERATURE

On account of the economic importance of grasshoppers a great deal of literature has accumulated since the initial researches in America of Riley, Packard, and Thomas (1877).

Papers that have been most suggestive for the present research are those of Carothers (1923), Hodge (1933), and Criddle (1933a). These investigators studied the feeding and egg laying behavior of a number of acridian species and tested the relations of proper diet to reproduction. As is the case in the investigations here discussed, Carothers and Criddle experimented chiefly with acridians that are not primarily of importance from the economic viewpoint.

[4] The geographical region in question, north central Texas, was in its primitive condition a level to rolling inland prairie. There are no marked variations in altitude. In such an inland region, general climatological conditions are much more uniform than in a mountainous area or even an area with very rough topography.

Recent researches involving problems of physiology, ecology, and control of chiefly economic species have been reported by Parker (1930, 1933), Shotwell (1930, 1935), Langford (1930), List (1934), Faure (1932), Uvarov (1928, 1931), Criddle (1933b), and others. Ecological studies have been made by Vestal (1913), Fox (1914), Morse (1920), and Strohecker (1937).

The extensive literature dealing with taxonomy and distribution of grasshoppers has many references in it to the behavior and feeding habits of grasshoppers. These also at times deal with local and regional distribution, as well as soil relations of individual species. These papers are chiefly the accumulation of field observations and include many of the papers of Hebard, Rehn, Morse, and Blatchley. Many aspects of the problem of *insect feeding* behavior have been investigated by Brues (1920, 1924, 1930, 1936).

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EXPERIMENTAL TECHNIQUE

Insectary Studies

In the experimental studies here undertaken, two major sub-problems were constantly in mind: (1) food preferences and (2) soil choices for oviposition. In controlled experiments attempting to duplicate environmental conditions, it is perfectly obvious that the nearer the experimenter can reproduce the conditions of the natural habitats the more nearly will his results represent conditions as they exist in nature. The cages used in the

[5] Preliminary Report on Food and Soil Relations of Three Species of Autumn Acridians by Frances Kelly and F. B. Isely. (Abstracts North Texas Biological Society, May 3, 1936).

writer's experiments here reported were designed with this in mind. These tests were conducted in an experimental garden and laboratory at the writer's residence (Figs. 2 and 3).

Cages—Figures 1 and 2 picture the types of cages employed. In large-scale grasshopper experimentation where many specimens are handled, it is necessary to use cages large enough to allow freedom of movement within the cage and small enough to afford opportunity for detailed observations of individual feeding, oviposition, and other behavior activities.

The cage shown in Figure 1 has much to recommend it. The frame and floor of the cage are made of well-seasoned yellow pine. The outside dimensions are 18 x 9 x 15 inches. The ends and back of the cages are covered with a good quality of 16-mesh galvanized screen. The front is

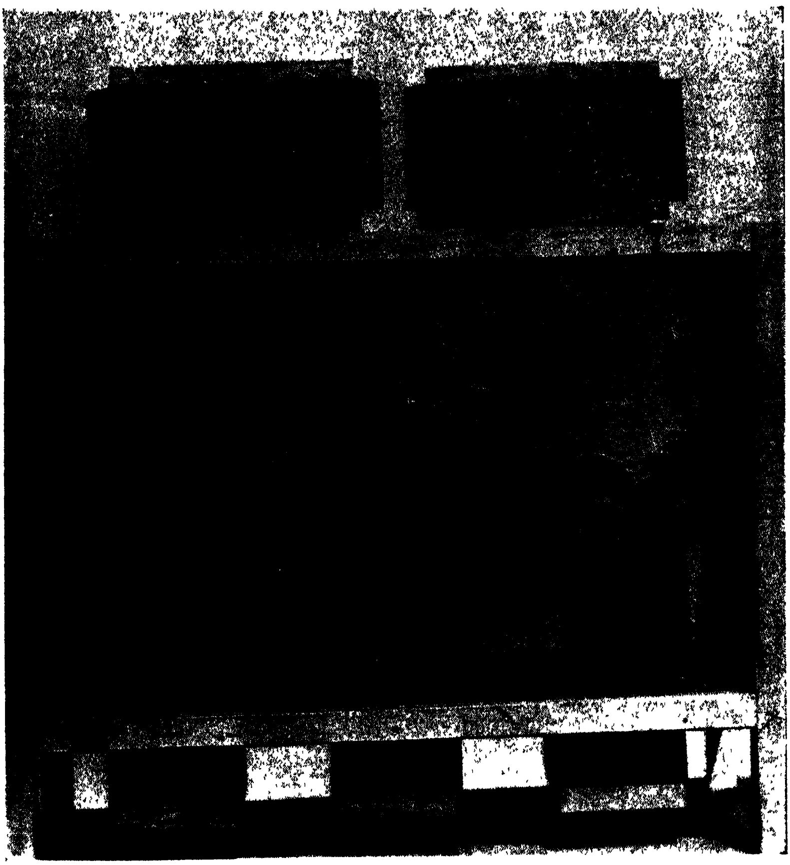

FIG. 1. Regulation cage with sliding glass door. The species shown is *Mermiria maculipennis maculipennis* Bruner. In this arrangement two of the soil pans are holding transplanted vegetation. In the center pan are three different soils as shown in the soil pan on top of the cage, upper right. The different soils were used to test acridian oviposition reactions.

closed with a sliding double strength glass which serves as the door of the cage. The glass front affords excellent opportunity to observe activities. The top and the floor are made of wood, the floor having three openings 5¾ x 3¼ inches into which galvanized pans 5½ x 3 x 3 inches fit. The pan dimensions do not include the flanges for support. These pans, although used for several purposes, are spoken of in my notes and in this paper as "soil pans." They were found convenient to hold bottles in which cut vegetation was placed in water for food. They also would hold small flower crocks with growing vegetation for food. Sometimes small blocks of soil with grasses or weeds were transplanted into the soil pans. Another important use was the holding of various soils for oviposition choices. In order to supply as wide a range of soils as possible in experiments for soil choices for oviposition, a double division was placed in the soil pan making three compartments for the different soils in a single pan. The compartment arrangement as well as different types of soils are shown in the two pans on top of the cage in Figure 1 and floor plan in Figure 6. This type of cage (Fig. 1) proved very convenient for making food changes. For sanitary reasons in regular routine food preference experiments where large numbers of adult specimens were used, it was found best to transfer specimens from one cage to another every second or third day to permit thorough cleaning of cages. Although we found no difficulty in maintaining seemingly healthful conditions, several species of acridians which we were studying apparently did not thrive in confinement.

Fig. 2. View of insectary (outdoor laboratory). Larger cages on two upper shelves, smaller cages, lower right.

A similar, smaller cage (Fig. 2, on the bottom shelf) was used for cage studies in the summer of 1935. During 1936-1937 these smaller cages were used when species of which only a few specimens were available for experimentation were handled.

Insectary—Shelter for the cages (Fig. 2) was a necessary feature. While the writer was trying to maintain essentially outdoor conditions, the cover of the shelter supplied needed shade for insects from the intense rays of the mid-day Texas sun and consequent excessive heat during high temperature periods. In the field some grasshoppers (Cyrtacanthacrinae and Acridinae) climb high into the vegetation on excessively hot July and August days. The Oedipodinae, however, are more likely to seek shade nearer the ground.

The insectary shelves afforded space for twenty-four cages. Additional work space was supplied by two tables with shelves underneath, used for cleaning cages and changing specimens.

In addition to the cages, as described above some observations were undertaken in still larger cages. A screened garden enclosure 12 x 30 feet, shown in the forefront of Figure 3, also gave opportunity for studying additional features of acridian behavior.

On account of other duties, the most active period for experimental work was during the months of June, July, and August. However, certain early spring species required study and observation in May, and other late summer species were best checked and observed during September and early

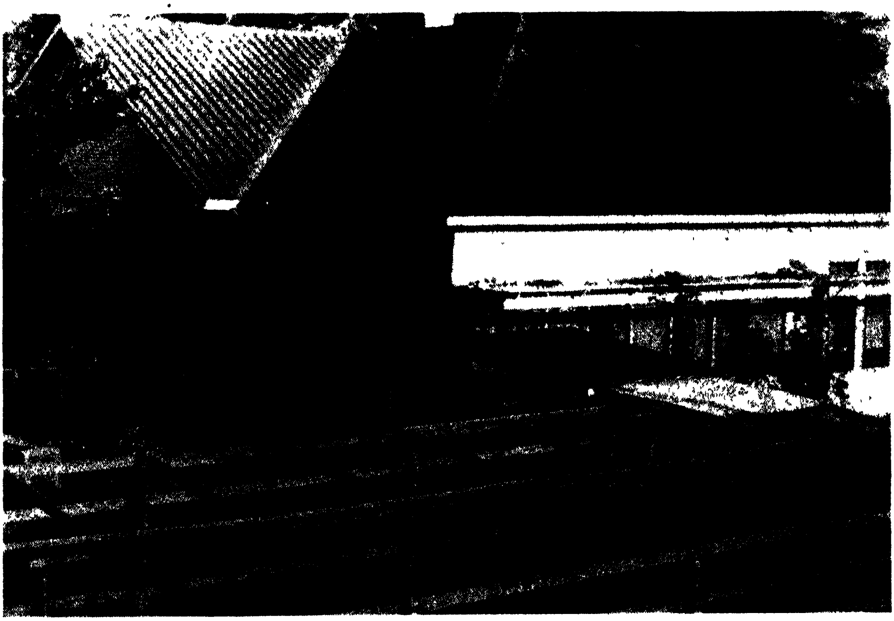

FIG. 3. Garden and Insectary. Screened garden enclosure in the forefront. Other special cages to the left of Insectary.

October. The range of experimentation and observation covered: (1) food choices, (2) feeding behavior, (3) soil choices for oviposition, (4) oviposition behavior, (5) sedentary stridulation,[6] (6) to a limited extent life history studies, and other behavior activities.

Species of Acrididae

In the various experiments undertaken, forty different species of acridians were used.[7] Adults collected directly from optimum habitats were preferred for behavior experiments although at times experimentation was carried on with late instar juveniles. It is obvious that for the experiments here undertaken, mature specimens fresh from their natural habitats would give the more typical reactions to the tests employed.

Host-Plants

The plant material used involved over 150 different species of the commonest native grasses, forbs,[8] garden, and crop plants. Many of the plants tested proved to be either unpalatable or unsuited to the dietary needs of the grasshopper species we were studying. In trying to analyze plant and acridian relations on the basis of habitat studies, it seemed obvious that the most important food plants would always be present in the optimum habitats of the various species being studied. However, for several acridian species it proved very difficult to determine a suitable host-plant. Many common acridians were strictly selective in their host-plant preferences. The difficulty of securing host-plants may be illustrated in my experiences with *M. impiger*. In 1936 cage studies *M. impiger* did not thrive. While able to maintain it (keep it alive in fair numbers) for a period of thirty days, the fact that only two packets of eggs were deposited was proof of faulty handling. It should be stated further that one of our difficulties with *M. impiger* was due in part to the fact that its optimum habitats were thirty miles distant from our laboratory. This made it difficult to test a complete series of possible host-plants from the optimum habitat of this species.

As already indicated, the researches of Carothers (1923, p. 8) and Criddle (1933, p. 478) make it evident that for certain acridians only a few plant species, essentially specific, will supply optimum dietary needs for normal growth and reproduction. On the other hand, there are several economic acridian species which are not so restricted. These grasshoppers are apparently adapted to a much wider range of plants (species) as food to meet their dietary requirements for development and reproduction. Hodge (1933, p. 326) shows clearly, however, that even *Melanoplus differentialis* (Thos.) will not develop normally on a restricted diet of oats or lettuce.

[6] Data concerning sedentary stridulation will be included in a later paper.

[7] During 1937 in addition to the acridian researches, behavior studies were made of several species of Tettigoniidae.

[8] The term forb is used to denote native herbs other than grasses (Clements 1929, p. 421). In this paper the terms broad-leaved plants, flowering plants (herbs), and forbs are used as equivalents.

RELATIONS OF ACRIDIDAE TO PLANTS

FOOD HABITS

Our food preference tests show that grasshoppers, like many other groups of insects, fall into three typical classes when experimentally checked for food choices: (1) Many species are oligophagous,[9] using as food only a limited number of plant species, the plants selected belonging frequently to a single family. (2) A few acridians are essentially monophagous, and their optimum dietary requirements are met by the use of a single plant species for food. (3) Polyphagous species, as would be expected, feed upon both grasses and forbs, and in general select their foods from a wide range of plant species. But even these grasshoppers under normal conditions show food preferences.

FOOD PREFERENCE TESTS

A description of a few typical experiments will make more significant the tabular data which is to follow. Figures 4 and 5 give a photographic record of food selection of characteristic species. The food plants shown on the right were photographed at 10:00 a.m., July 31, 1936. After the picture was

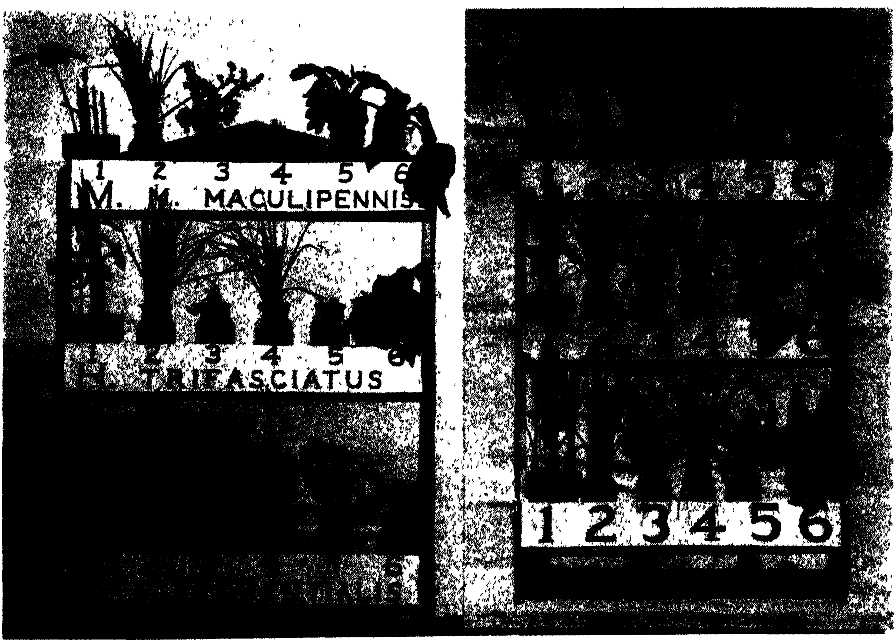

FIG. 4. Photographic record showing food choices of three mid-summer acridians. Identical plant foods were offered to each species as shown on the right. The plants eaten and the results of feeding of each species, 24 hours later, shown on the left.

[9] "Restricting itself to the members of related plant orders, of a single order, of a single family or even a single genus." (Folsom and Wardle 1934, p. 258).

taken each of the three series of the six different plants was placed in an experimental cage (Fig. 1). Each of these cages contained 25 specimens of one of the three species. The species are named in the left half of Figure 4. The record of the sexes was not definitely checked, but the numbers of males and females were approximately the same. The plants used were as follows: (1) Seedlings grown in a flower pot: cotton (Gossypium), corn (Zea), and wheat (Triticum). The height of the corn seedlings made it necessary to clip the top leaves in order to fit the shelf space used for holding plants to be photographed.

Cut shoots and leaves of the five other food plants were placed in water in bottles when offered as food. These, with the numbers to which they correspond in the figure, are as follows:

(2) Silver beardgrass—*Andropogon saccharoides* Swartz
(3) Small leaved spurge—*Euphorbia* sp.
(4) Bermuda grass—*Cynodon dactylon* (L.) Pers.
(5) Oval leaved spurge—*Euphorbia nutans* Lag.
(6) Sunflower—*Helianthus annuus* L.

After twenty-four hours the food plants used in the experiment were again photographed, with the results shown on the left (Fig. 4).

Mermiria maculipennis maculipennis Bruner fed almost exclusively on Bermuda grass, the vegetation in bottle No. 4. Second choices were the wheat seedlings and the leaves of the corn growing in the flower pot (No. 1). There was some feeding on the Andropogon (No. 2). The cotton in flower pot No. 1 and the cut shoots of the Euphorbias and sunflower in bottles 3, 5, and 6 were untouched.

Hadrotettix trifasciatus (Say) fed especially on the two species of Euphorbia (Nos. 3 and 5). The figure shows that the vegetation in these plants was eaten to the rim of the bottles. Other vegetation was untouched. These two spurges are not usually found in the optimum habitats of *H. trifasciatus.* This feeding behavior represents a good case of adaptation to new food plants under cage environments.

The first choice of *Melanoplus differentialis* (Thos.) centered around the cultivated crop plants growing in the flower pot (No. 1). There was considerable feeding on the sunflower (No. 6) and on Euphorbia (No. 3). There was a little feeding on Andropogon (No. 2). Bermuda grass (No. 4) and *E. nutans* (No. 5) were untouched.

The set-up for the experiments, for which Figure 5 is a photographic record, represents the feeding activities of four species that reach their *adult peak* in north central Texas in August.

In these experiments an identical set-up of plant foods was arranged and photographed as shown in bottles in Figure 5, upper left Nos. 1-6. Unfortunately Nos. 3 and 5 in the upper left were reversed in the arrangement shown in the upper right. The upper right photograph merely shows the

way in which the plants were placed in the soil pans. The significant numbers to be studied for comparison are the ones shown in the upper left series. The plants used were as follows:

(1) Broomweed—*Amphiachyris dracunculoides* (DC.) Nutt.
(2) Johnson grass—*Sorghum halepense* (L.) Pers.
(3) Common ragweed—*Ambrosia psilostachya* DC.
(4) Silver beardgrass—*Andropogon saccharoides* Swartz.
(5) Giant ragweed—*Ambrosia aptera* DC.
(6) Bermuda grass—*Cynodon dactylon* (L.) Pers.

The photographed series (Fig. 5) was set up September 29, 1936. Similar set-ups of food plants as nearly identical as possible were placed with each of the four acridian species in four separate standard cages. The numbers of specimens used were as follows:

Syrbula admirabilis Uhler—12

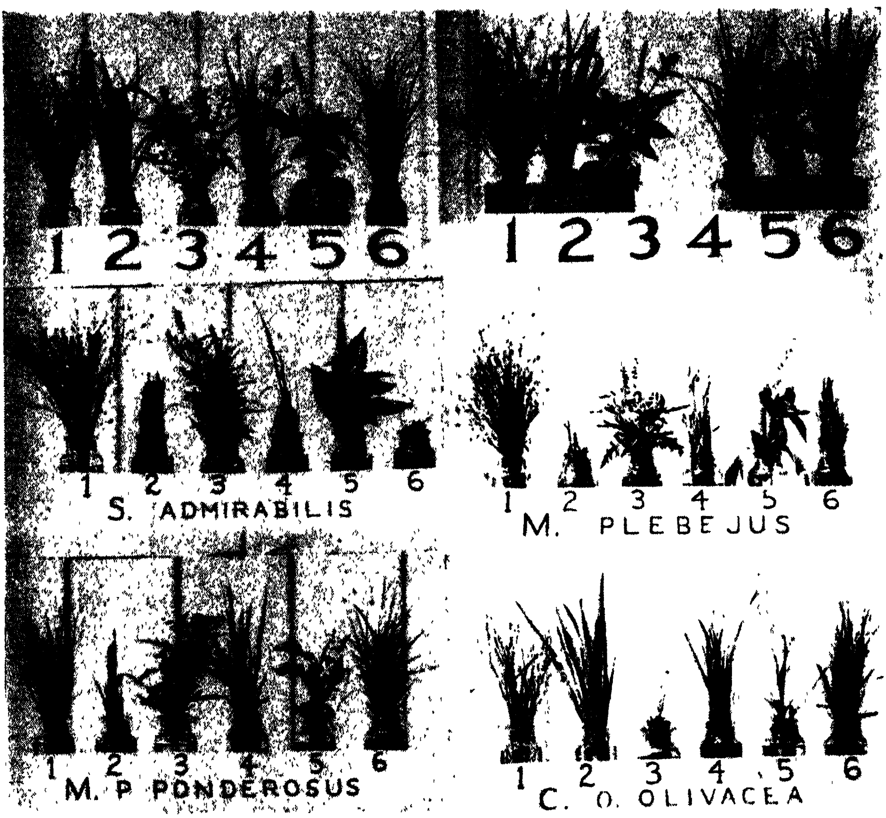

FIG. 5. Photographic record showing the feeding activities of four species of grasshoppers which reach their adult peak in north central Texas in August. Typical plant arrangement upper left. Food bottles in soil pans, upper right. The plants eaten and those not eaten are shown below and arranged in same order as 1-6 upper left.

Melanoplus plebejus (Stål)—14
Melanoplus ponderosus ponderosus Sc.—11
Campylacantha olivacea olivacea Sc.—14

Most of these specimens were females. Soon after this series of experiments was arranged (September 29) the weather became unfavorable, turning cold and rainy. For the first three days the grasshoppers were more or less dormant, but with sunshine and warm weather on the fourth day (October 2) feeding activities were renewed. The food preference results (Fig. 5) were photographed at noon, October 3. The appearance of the control set-up of plants and the plants not eaten in the cages shows that the vegetation kept fresh and in good condition during the period of experimentation (September 29-October 3).

The first choice of *Syrbula admirabilis* Uhler was Bermuda grass (No. 6). After the Bermuda grass was eaten *S. admirabilis* fed on Andropogon (No. 4) and Johnson grass (No. 2). This species did not touch the forbs.

Melanoplus plebejus (Stål) showed a definite preference for Johnson grass (No. 2). Second choices were Andropogon (No. 4) and Bermuda grass (No. 6). All of its food plants were grasses.

Melanoplus ponderosus ponderosus Sc.—This species is a flower and fruit feeder. Flowers and fruit were stripped from broomweed (No. 1) and giant ragweed (No. 5). However, this species did not touch the common ragweed (No. 3). It fed to an extent on the foliage of the plants of Johnson grass (No. 2) and giant ragweed (No. 5).

Campylacantha olivacea olivacea Sc.—This species also feeds on flowers and fruit. It stripped the flowers and fruit from broomweed (No. 1), common ragweed (No. 3), and giant ragweed (No. 5). First choice foliage for *C. o. olivacea* was *Ambrosia psilostachya* DC. This common ragweed was usually untouched in the other acridian cages in our continuous series of food preference experiments. This widely distributed plant, however, is a coarse, sturdy weed which is used quite extensively by several acridian species for roosting and shelter. Even in the cage occupied by *Syrbula admirabilis* Uhler (Fig. 5), although the grasses were used as food, roosting, when the grasshoppers were inactive, was done on the cut shoots of the two ragweeds.

DETAILED EXPERIMENTAL STUDY OF ACRIDIAN HOST-PLANT PREFERENCES

Organization of Data

The foregoing account (Food Preference Tests) and the photographic records should serve to make clear the data pertaining to food choices given in Tables 1-3. The abbreviations used in the tables are explained in connection with a complete listing of Acrididae and host-plant species.

All plants specifically listed in the tables were found to be acceptable food for one or more species of grasshoppers. Host-plants listed for Table 1 are not repeated in the additional host-plant species listed for later tables. Terms and keys used in Tables 1-3 are fully explained in a general account preceding Table 1. The key meanings are briefly repeated in connection with each table.

FORM OF PLANT FOOD

As a rule the food was supplied in the form of cut shoots of grasses and forbs. The cut shoots were immediately placed in bottles of water after being cut. Sometimes the food was changed during the day, but usually only once daily.

Crop Plants. On account of possible economic importance, crop plants, especially wheat, corn, and cotton were always checked as to their acceptability as food. Crop plants as food were offered in two forms: (1) as cut shoots and, more frequently, (2) as seedlings in small flower pots. Since the reactions of the acridians were essentially similar, these differences in the crop-plant food materials are not taken into account in the tables. In the discussion of individual species, differences in reaction may be noted. The determined host-plants of experimental species were offered, as nearly as possible, as food to other acridians being checked at the same time for food choices. Since the chief experimental work was in progress for six months of the year, many native weeds and grasses were not in season at the time a specific acridian species was being studied. As a result, host-plants of one species were not always available to be offered to other species being tested.

TERMS USED IN TABLES 1-3

HP—Host-Plant. This designation is used for plants which were *repeatedly selected as food* by an acridian being tested. It also means that the plant species is *available in the optimum habitats* of this acridian as determined by field studies.

PH—Primary Host. Cage and field studies in several instances pointed to specific plant species as essential to maintenance of certain acridian species. These plants are designated as primary hosts.

1—First Choice. This designation means that the food plant was eaten in preference to all others by the acridian species being tested. It may include host-plants, but usually host-plants are designated by HP. Primary host-plants naturally would be first choice. If they were found to be primary host-plants, they are designated by PH in the tables.

1-2, 1-3. These designations indicate that the plant species was eaten freely. The order of preference may have been variable in our long series of tests. Several species were under observation in cages for over two months in one season. Others were rechecked for food preferences three different years. The 1-2, 1-3 designations are especially used for crop-plant preferences.

2—Second Choice. If food plant No. 1 was available in a cage, a plant freely eaten after the supply of No. 1 was exhausted is designated as choice No. 2. For some of our tests No. 2 is apparently one of the host-plants of the species being tested.

3—Third Choice. Third choice plants are probably not especially desirable for the species in question. Third choice means that these plants were eaten when other more desirable food was no longer available.

St—Starved with this plant available. These data were secured from starvation experiments, Tables 4-6.

N—Nibbled. The term nibbled is reserved for plants that were eaten very sparingly or barely nibbled.

R—Refused. The term refused is used for plants that were not eaten. In our tests certain acridian species absolutely refused many different plant species offered as food.

Fl—Flowers. Flowers, especially ray and disk flowers of Compositae, were eagerly eaten by several grasshopper species.

Fr—Fruit. A few species fed on immature fruit, usually along with foliage.

Others Refused. Since lack of space prevents the listing of all of the plant species tested, the designation "Others Refused" affords opportunity to show in the tables the total number of plant species offered as food. With the exception of crop plants, as a rule only plants from optimum habitats of an acridian species were offered. However, plants acceptable to other acridian species, and available, were usually tested.

Others Eaten. These are also plants that are not listed in the tables and figure only in the totals of plants species offered. Here are included garden plants, grasses, and weeds easily available.

Number of Days Studied. The total days an individual species was under observation in cage tests is given.

Since there is an evident parallel between feeding behavior and subfamily grouping, advantage has been taken of this correlation in arranging the food preference data which follow under the three different acridian subfamilies concerned.

ACRIDINAE

HOST-PLANTS OF ACRIDINAE

The probable host-plants were selected by making field lists[10] of available plants in optimum habitats of the grasshoppers being experimentally checked for food choices. Many plants were offered as food which were universally refused in routine tests. Time was not available to resort to starvation tests with many of these plants which were rejected. Only the totals of the plant species which proved wholly unpalatable are given in connection with the tables.

[10] Identifications of host-plant species were checked by comparison with herbarium specimens identified by plant taxonomists.

In the tables the plant species are usually listed by their generic names. However, crop plants and certain well known grasses and weeds are listed by common name (Bermuda grass, Johnson grass, broomweed, sunflower, etc.).

MONOCOTYLEDONS—*Species*	*Common Name*
Andropogon furcatus Muhl	Bluejoint Turkeyfoot
Andropogon saccharoides Swartz	Silver Beardgrass
Cynodon dactylon (L.) Pers.	Bermuda Grass
Stipa leucotricha Trin. and Rupr.	Texas Needlegrass
Sorghum halepense (L.) Pers.	Johnson Grass
Sporobolus heterolepis A. Gray	Prairie Dropseed
CROP PLANTS	
Triticum sp.	Wheat
Saccharum officinarum L.	Sugarcane
Zea mays L.	Maize, Indian corn
DICOTYLEDONS	
Evax multicaulis DC.	Indian Tobacco
Amphiachyris dracunculoides (DC.) Nutt.	Broomweed
Helianthus annuus L.	Sunflower
Plantago sp.	Plantain
CROP PLANTS	
Gossypium hirsutum L.	Cotton

The plants listed above were found to be acceptable food for at least one of the ten different acridian species listed below.

In the series of experiments with these Acridinae eight additional monocotyledons and fourteen additional dicotyledons were repeatedly offered as food to several species of the Acridinae and were refused.

SLANT-FACED GRASSHOPPERS—ACRIDINAE

Species	*Abbreviations in Table*
1. *Mermiria maculipennis maculipennis* Bruner	M. mac.
2. *Mesochloa abortiva* Bruner	
3. *Acrolophitus variegatus* (Thos.)	A. var.
4. *Syrbula admirabilis* Uhler	S. ad.
5. *Amphitornus coloradus* (Thos.)	
6. *Orphulella speciosa* (Sc.)	
7. *Geneotettix deorum* (Sc.)	G. deo.
8. *Boopedon nubilum* (Sc.)	B. nub.
9. *Boopedon maculatum* Caudell	B. mac.
10. *Boopedon auriventris* McNeill	B. aur.

The feeding reactions of the seven of these species of the Acridinae indicated by abbreviations are tabulated in Table 1. Further discussion of feeding behavior follows the table.

TABLE 1. FOOD PREFERENCES OF ACRIDINAE

HP —Host-Plant
PH —Primary Host.
1 —First Choice
1-2, 1-3—Eaten in absence of 1 or HP.
2 —Second Choice.
St —Starved
N —Nibbled
R —Refused.
-- —Not tested.

Acridinae Tested	M. mac.	A. var.	S. ad.	G. deo.	B. nub.	B. mac.	B. aur.
Number of days studied	64	62	47	46	19	25	4
PLANTS TESTED							
A. furcatus	2	R	2	--	N	1-3	HP
A. saccharoides	2	R	2	N	R	1-3	PH
Bermuda grass	1	R	1	1	HP	HP	?
Stipa	1-3	R	2	--	N	1-3	--
Johnson grass	1-2	N	1-3	1-3	N,R	1-2	N
S. heterolepis	HP	--	2	2	--	--	--
Crop Plants							
Wheat	1-2	St	1-2	1-2	R	1-2	--
Cane	1-3	St	1-3	1-3	--	--	--
Corn	1-3	R	1-3	1-3	--	--	--
Forbs							
Evax multicaulis	R	PH	--	--	--	--	--
Broomweed	St	--	St	R	R	R	--
Sunflower	St	R	St	R	R	R	R
Plantigo	--	2	--	--	--	--	--
Crop Plants							
Cotton	R	R	R	R	R	R	--
Total Eaten	8	4	8	5	1	6	3
Total Refused, Nibbled, Starved	4	8	3	4	8	3	2
Others Refused (Not in table)	26	11	15	5	2	6	4
Others Eaten (Not in table)	6	2	2	0	2	4	1
Grand Total	44	25	28	14	13	19	10

FEEDING BEHAVIOR OF THE ACRIDINAE

The ten species of the sub-family Acridinae studied in food tests show a 90% preference for grasses as host-plants. Bermuda grass easily ranks as the first choice. The preference for Bermuda grass[11] on the part of our Acridinae was acquired. It is obvious, as already suggested, that vegetation ***absent in typical virgin, optimum habitats*** of a species can not, as a matter of course, belong to the original basic food requirements of the species.

Some of the facts of our feeding behavior studies are represented in a brief review of the feeding activities of *Mermiria maculipennis maculipennis* Bruner. This characteristic blackland prairie species was under constant

[11] Miss Agnes Chase, Senior Agrostologist, Bureau of Plant Industry, writes under date of July 30, 1937: "Bermuda grass, *Cynodon dactylon* (L.) Pers., must have been introduced with the first Spanish explorers." "The first record I find of Cynodon in America is in Pursh's Flora Americae Septentrionalis, 1814. He says, 'on roadsides and in cultivated ground frequent.' "

observation in cages from the time it reached maturity, June 24, to August 4, 1936. Preliminary studies of this species had already been made in 1935, and a brief recheck was made in 1937. *M. m. maculipennis* was given a thorough testing in our experiments for both food preferences and soil choices in oviposition. During the 1936 studies about thirty individuals were constantly maintained in a single cage (Fig. 1). In their optimum habitats the Andropogons (*A. furcatus* and *A. saccharoides*) afford shelter and roosting surfaces for these agile, elongated, slant-faced grasshoppers. The Andropogons undoubtedly are the important field index plants of *M. m. maculipennis*. While they are acceptable as food they are not the primary host-plants if the results of cage studies are taken as evidence.

In cages *Mermiria m. maculipennis* definitely chose Bermuda grass and Sporobolus for food in preference to either of the species of Andropogon. In some tests it appeared that young leaves of Johnson grass were more largely eaten than the Andropogons.

On July 22, and again on July 24 and 29, 1937 I made a thorough examination of a recently discovered habitat, a long, narrow strip of railroad right-of-way[12] blackland prairie land. For a distance of about five yards on either side of the railroad tracks the made-soil was covered with a heavy stand of Johnson grass with a few intermixed weeds. This inner strip on either side of the railroad track is the ground that is continually disturbed in upkeep-operations of the railroad section hands, such as cutting of weeds and grading. Outside of this inner belt was a strip five to eight yards in width of undisturbed prairie land.[13] The vegetation of this outer belt was predominantly native grasses mixed with weeds. *Mermiria maculipennis maculipennis* Bruner was fairly abundant in this outer belt. The inner belt of Johnson grass was inhabited by larger numbers of *Melanoplus differentialis* (Thos.). Infrequent representatives of several other acridians were noted. The differences in distribution were clean-cut. The *M. m. maculipennis* were feeding by preference on native grasses (Sporobolus, Andropogon, grama). The *M. differentialis* were using as food some Johnson grass but especially the mixed weeds of this inner belt. These field observations are given with some detail to emphasize the fact that cage results[14] need to be counter-checked with field observations.

An exceptional species among our Acridinae from the viewpoint of food preferences was *Acrolophitus variegatus* (Thos.). In Manitoba, Canada, Criddle (1933, p. 481) reports *A. hirtipes* (Say) feeding by preference on the Boraginaceae. During 1935 it was difficult to maintain *A. variegatus*

[12] A railroad right-of-way field station has in itself many artificial restrictions when viewed as a natural environment.

[13] The once virgin blackland prairie of north central Texas is now nearly wholly given over to agriculture.

[14] In special cages (40 x 20 x 30 inches high) and in larger soil pans blocks of soil of Andropogon and Sporobolus were transplanted in one end and Johnson and sunflower blocks in the other end. Forty specimens of each species were placed in this cage. Over 80 per cent of the *Mermiria maculipennis maculipennis* Bruner selected the Andropogon end of the cage while the *Melanoplus differentialis* (Thos.) showed an even stronger preference for the Johnson grass end. The test suggested the advantage of larger cages for behavior studies.

successfully in cages on a diet of various grasses and forbs. May 16, 1936 on a field study trip I observed a small colony of fifth instar juveniles associated with *Evax multicaulis* DC. Cage tests and repeated field observations proved this plant to be the primary host-plant of *A. variegatus*. Plantain (Plantago) is a second choice food plant for this species.

An excerpt from my field and laboratory notes will further suggest the need of correlation between field and laboratory studies. Field Station, Lancaster, Dallas County, Texas, May 16, 1936: "After a thorough examination of the flora of what appears to be an optimum habitat of *A. variegatus* it appears that Indian tobacco (*Evax multicaulis* DC.) should be given tests as a likely food for this species. The juvenile and the adult color pattern of this acridian with its pale green ground-color, mottled with white and the white woolly stems and the broad leaves of Evax suggest a background which fits very well into the general picture of protective coloration."

Laboratory notes, May 20, 1936: "After four days testing with fifteen specimens freshly brought in from the field, it is clear that *A. variegatus* feeds by choice and perhaps almost exclusively in its juvenile stages on Evax. All of its feeding for a period of four days has been exclusively on Evax, and as nearly as can be determined not a nibble has been taken off of the various grasses and other forbs in the food bottles in the cage."

Syrbula admirabilis Uhler—This is one of the most generally distributed late summer and fall grasshoppers in our area. The results of experimental studies suggest that it is a general grass feeder. Bermuda grass is ranked as the first choice and *S. admirabilis* is often found associated with Bermuda grass in nature. It is also frequently associated with Andropogon and Sporobolus.

Geneotettix deorum (Sc.) is one of the most widely distributed summer and early fall acridians. However, in north central Texas it seldom becomes abundant in any single locality. Bermuda grass was ranked as first choice in cage tests but all of the field data suggest that *G. deorum* has a wider choice of grasses than our experimental data would indicate.

Little can be added to the facts in the table concerning the Boopedona. These three species were not as extensively studied as some of the others. *Boopedon auriventris* McNeill is of interest in that it was one of two grass feeding species which in cage tests did not select Bermuda grass as its first choice.

In addition to the seven species listed in the table, food choice studies were undertaken with *Mesochloa abortiva* Bruner, *Amphitornus coloradus* (Thos.), and *Orphulella speciosa* (Sc.). As the series of checked experiments was not as extensive as for the other seven Acridinae, details are not given in the tables. These relatively small Acridinae belong definitely to the grass feeders with Bermuda grass ranking as first choice. In the case of *O. speciosa* Bermuda grass appears to be the present host species in north central Texas.

OEDIPODINAE AND BATRACHOTETRIGINAE

ADDITIONAL HOST-PLANTS OF THE OEDIPODINAE

MONOCOTYLEDONS—*Species*	*Common Name*
Aristida purpurea Nutt.	Purple Three-Awn
Bromus catharticus Vahl.	Rescue Grass
Cenchrus sp.	Sandbur
DICOTYLEDONS	
Gaillardia pulchella Foug.	Indian Daisy
Salvia farinacea Benth.	Blue Salvia
Monarda clinopolioides A. Gray	Horse Mint
Asclepiodora decumbens (Nutt.) A. Gray	Milkweed
Euphorbia sp.	Small leaved spurge
Euphorbia nutans Lag.	Oval leaved spurge
Jatropha stimulosa Michx.	Bull nettle
Houstonia angustifolia Michx.	Houstonia
Hymenopappus corymbosus T. & G.	Hymenopappus
Ambrosia psilostachya DC.	Common ragweed
Ambrosia aptera DC.	Giant ragweed

For other plant species listed in Table 2 see plants previously listed for Table 1.

BAND-WINGED GRASSHOPPERS—OEDIPODINAE

Species	*Abbreviations in Table*
1. *Arphia simplex* SC.	A. sim.
2. *Chortophaga viridifasciata* (DeGeer)	
3. *Encoptolophus subgracilis* Caudell	
4. *Encoptolophus sordidus costalis* (Sc.)	
5. *Hippiscus rugosus* (Sc.)	
6. *Pardalophora saussurei* (Sc.)	P. sauss.
7. *Xanthippus corallipes pantherinus* (Sc.)	X. c. p.
8. *Spharagemon collare cristatum* (Sc.)	S. cris.
9. *Trachyrhachis kiowa fuscifrons* (Stål)	
10. *Trimerotropis citrina* Sc.	
11. *Trimerotropis pistrinaria* Sauss.	T. pist.
12. *Hadrotettix trifasciatus* (Say)	H. tri.

LUBBER GRASSHOPPER—BATRACHOTETRIGINAE

1. *Brachystola magna* (Girard)

The food preferences of six of the above Oedipodinae are shown in Table 2. The other species are included in the discussion that follows Table 2.

FEEDING BEHAVIOR OF THE OEDIPODINAE AND BATRACHOTETRIGINAE

The Oedipodinae listed in Table 2 were given a rather thorough checking as to their food preferences. Three species are primarily grass feeders: *Arphia simplex* Sc., *Pardalophora saussurei* (Sc.), and *Xanthippus corallipes pantherinus* (Sc.). Two others, *Trimerotropis pistrinaria* Sauss. and

Table 2. Food Preferences of Oedipodinae

HP —Host-Plant.
PH —Primary Host.
1 —First Choice.
1-2,1-3—Eaten in absence of 1 or HP.
2 —Second Choice.
3 —Third Choice.
St —Starved.
N —Nibbled.
R —Refused.
-- —Not tested.

Oedipodinae Tested	A. sim.	P. sauss.	X. c. p.	S. cris.	T. pist.	H. tri.
Number Days Studied	62	104	98	30	92	83
Plants Tested						
Grasses						
A. furcatus	N	1-3	N	2	R	R
A. saccharoides	1-2	1-3	HP	2	St	R
Aristida purpurea	1-2	1-3	HP	N	N	N
Bromus catharticus	1-2	1-3	1-3	--	--	--
Bermuda grass	1	1	1	1	3	3
Stipa	HP	1-3	1-3	1-2	--	R
Johnson grass	1-2	1	1-3	1	3	3
Sandbur	--	1	--	1-3	--	--
Crop Plants						
Wheat	1	1-2	1-3	1-3	2	3
Corn	1-2	1-3	N	N	R	N
Forbs						
Sunflower	N	N	N	N	St	N
Broomweed	R	R	N	--	St	St
Gaillardia	R	R	R	--	2	N
Monarda	R	R	R	R	--	R
A. decumbens	R	--	R	--	R	HP
Bull nettle	--	N	--	1-2	--	--
Houstonia	R	--	--	--	HP	HP
Hymenopappus	R	--	--	--	PH	R
Common Ragweed	St	--	R	--	St	St
Giant Ragweed	St	R	R	R	N	St
Crop Plants						
Cotton	R	N	N	1-3	N	N
Total Eaten	8	10	7	9	5	3
Total Nibbled, Refused, Starved	11	7	10	5	10	13
Others Refused (Not in table)	21	16	8	8	8	34
Others Eaten (Not in table)	9	9	11	7	7	11
Grand Total	39	42	36	29	40	51

Hadrotettix trifasciatus (Say) definitely select the foliage of certain dicotyledons as food. *Spharagemon collare cristatum* (Sc.), to the extent of our tests, should be classed as a mixed feeder, that is, selecting both grasses and forbs.

Stipa leucotricha Trin. and Rupr. is clearly the major host-plant in optimum habitats of *A. simplex*. *A. simplex* in north central Texas hatches with the fall rains usually in September and early October. It passes the period from October to March as a first instar juvenile. Shelter undoubted-

ly plays a very important role in affording favorable environmental conditions for this species. *A. simplex* is a strong direct flier and in its adult stage is rather widely distributed. The juveniles, however, are found in large numbers only in open woods and timber margins.

Xanthippus corallipes pantherinus (Sc.) passes its first instar stages, September to April, in exposed situations. Thin soil (Houston stony clay shallow phase), hill tops and eroded (subsoil) slopes are the selected sites for egg laying. The juveniles through the various instars apparently remain near the hatching sites. As adults, however, *X. c. pantherinus* seeks the taller vegetation. This species is noteworthy as a strong, direct flying species.

The feeding behavior of *Pardalophora saussurei* (Sc.) paralleled very closely that of *X. c. pantherinus*. However, the optimum habitats of these two species are very different. In the second section of this paper the reasons for differing habitats of *X. c. pantherinus* and *P. saussurei* will be discussed.

Continued and persistent studies were carried on with *Trimerotropis pistrinaria* Sauss. and *Hadrotettix trifasciatus* (Say). *T. pistrinaria* is limited in its field distribution to eroded subsoils. It is able to exist apparently on a very sparse diet. As shown in the table, Hymenopappus served as a host-plant of this species. This plant is abundant in the optimum habitats of *T. pistrinaria*. Houstonia was the No. 2 choice from among a large group of plants offered to *T. pistrinaria*. Field behavior of *T. pistrinaria* is of interest. It belongs to that group of acridians that circle back in their flight thus showing a definite site-selection. The "circle back" type of flight behavior is characteristic of those acridians that stick rather closely to their specific soil backgrounds as adults. In contrast with these we have such species as *A. simplex*, *X. c. pantherinus* among the Oedipodinae, and *Mermiria maculipennis maculipennis* Bruner among the Acridinae, which usually fly straight away when flushed. The latter species are more likely to become widely scattered as adults.

Hadrotettix trifasciatus (Say) is somewhat similar in its choice of habitat to *Trimerotropis pistrinaria* Sauss., but ranges more widely. Our field studies pointed out *Asclepiodora decumbens* (Nutt.) A. Gray and *Houstonia angustifolia* Michx. likely food selections. Later cage studies proved that these plants were eagerly fed upon by *H. trifasciatus*. In spite of long and persistent experimentation, there still remains a great deal to be done in determining the host-plants of this species.

Six other Oedipodinae were checked for food preferences. Cage tests were carried on with these species for only brief periods, but the records show that all six species are essentially grass feeders. Further study will doubtless bring out significant variations. *Encoptolophus subgracilis* Caudell is of special interest because it is the only grasshopper in our area that confines its activities to cultivated fields. In our cages it fed on the grasses growing as weeds in field margins and to a limited extent on the leaves of

cotton. However, the damage it does to the cotton is negligible. *Trimerotropis citrina* Sc. also is a mixed feeder. Bermuda grass, Parthenium, giant ragweed, and broomweed were found to be acceptable food plants for *T. citrina*.

In our cages *Encoptolophus sordidus costalis* (Sc.), *Chortophaga viridifasciata* (DeGeer), *Hippiscus rugosus* (Sc.), and *Trachyrhachis kiowa fuscifrons* (Stål) fed chiefly on grasses.

Brachystola magna (Girard) is one of the economic species of certain areas of Texas. In the field it is very definitely associated with coarse weeds and in the cages fed by preference on cotton, sunflower and giant ragweed.

CYRTACANTHACRINAE

Additional Host-Plants of Cyrtacanthacrinae

Dicotyledons—*Species*	*Common Name*
Centaurea americana Nutt.	Star Thistle
Thelesperma trifidum (Poir.) Britton	
Engelmannia pinnatifida T. & G.	
Baccharis texana (T. & G.) Gray	Dactylotum weed
Aster exilis	Aster
Grindelia	Gumweed
Parthenium hysterophorus L.	Parthenium

For other plants listed in Table 3 see lists of plants given in connection with Tables 1 and 2.

Spine-Breasted Grasshopper—Cyrtacanthacrinae

Species	*Abbreviations in Table*
1. *Hypochlora alba* (Dodge)	
2. *Paraidemona punctata* (Stål)	P. punc.
3. *Campylacantha olivacea olivacea* Sc.	C. o. o.
4. *Hesperotettix viridis viridis* (Thos.)	H. v v.
5. *Hesperotettix speciosus* (Sc.)	H. spec.
6. *Melanoplus scudderi latus* Morse	
7. *Melanoplus texanus* (Sc.)	M. tex.
8. *Melanoplus plebejus* (Stål)	M. pleb.
9. *Melanoplus discolor* (Sc.)	
10. *Melanoplus flabellatus* (Sc.)	M. flab.
11. *Melanoplus differentialis* (Thos.)	M. dif.
12. *Melanoplus ponderosus ponderosus* (Sc.)	M. pon.
13. *Melanoplus confusus* (Sc.)	M. con.
14. *Melanoplus mexicanus mexicanus* (Sauss.)	
15. *Melanoplus keeleri keeleri* (Thos.)	
16. *Melanoplus impiger* (Sc.)	M. imp.
17. *Dactylotum pictum* (Thos.)	D. pic.

Feeding Behavior of the Cyrtacanthacrinae

Many of the Cyrtacanthacrinae tested in our cages proved to be almost entirely selective feeders. Of the twelve species shown in Table 3 all but

TABLE 3. FOOD PREFERENCES OF CYRTACANTHACRINAE

HP —Host-Plant.
PH —Primary Host.
1 —First Choice.
1-2, 1-3—Eaten in absence of 1 or HP.
2 —Second Choice.
3 —Third Choice.
St —Starved.
N —Nibbled.
R —Refused.
Fl —Flowers.
Fr —Fruit.
-- —Not tested

Cyrtacanthacrinae Tested	P. punc.	C. o. o.	H. v. v.	H. spec.	M. tex.	M. pleb.	M. flab.	M. dif.	M. pon.	M. con.	M. imp.	D. pic.
Number Days Studied	48	46	67	66	56	29	46	55	49	42	52	51
PLANTS TESTED												
Grasses												
A. saccharoides	St	St	St	St	St	2	R	N	R	St	R	R
Bermuda grass	St	N	St	St	St	1–3	2	3	3	St	R	R
Stipa	R,N	--	--	--	R	--	N	N	--	St	R	R
Johnson grass	R,N	R	R	R	3	1	3	HP	2	3	N	N
Crop Plants												
Wheat	N	--	R	R	3	--	2	1–3	--	1–3	1–3	3
Corn	1–3	--	R	R	3	2	3	1–3	2	N	1–3	3
Forbs												
Broomweed	3	Fl	HP	--	3	Fl	N	1–3	Fl	--	N	3
Centaurea	R	--	--	R	3	--	Fl	1–3	--	N	1–3	--
Gaillardia	HP	--	N	N	HP	3	N	1–3	N	Fl,N	Fr 3	--
Thelesperma	HP	--	--	--	2	R	--	--	R	Fl Fr	R	--
Engelmannia	2	--	--	--	3	--	HP	R	--	--	--	--
Baccharis	N	R	R	--	N	R	--	N	R	--	--	PH
Aster	--	R	1–3	1–3	--	3	3	1–3	3	--	3	HP
Grindella	R	R	HP	N	R	R	N	1–3	R	--	R	R
Parthenium	--	--	R	N	--	2	1–2	1–3	2	--	2	R
Sunflower	1–3	Fl 1–3	R	HP	1–3	R	3	HP	3	1–3	3	N
Monarda	R	--	R	N	3	--	N	1–3	--	--	1–3	--
Plantago	HP	--	--	--	HP	--	3	--	--	1–3	2	1
Common ragweed	--	Fl HP	St	N	R	R	R	N	N	R	R	R
Giant Ragweed	R	Fl 1–3	3	HP	N	2	N	HP	Fl Fr	3	R	N
Crop Plants												
Cotton	3	R	R	2	N	2	2	1	2	--	1–3	3
Total Eaten	5	4	4	5	11	10	11	14	9	7	10	7
Total Nibbled and Refused	10	7	12	10	8	5	8	5	6	6	9	8
Others Refused (Not in table)	18	4	15	13	12	4	7	15	2	8	13	5
Others Eaten (Not in table)	4	--	1	4	6	6	6	21	0	9	14	3
Grand Totals	37	15	32	32	37	25	32	55	17	30	46	23

one select their host-plants from among the dicotyledons. The major selections were made from among the Compositae. Only two other dicotyledonous families appear in the Table 3 list, Labiateae, represented by Monarda, and Plantaginaceae, represented by Plantago. The leaves alone are not chosen for food, but several species have a tendency to feed on the flowers and in a few cases on the fruit of flowering plants.

Melanoplus differentialis (Thos.), as one of the chief economic grasshoppers of the central states, has been extensively studied by economic entomologists with reference to its food habits. In our cages *M. differentialis* proved to have a striking preference for crop plants, especially cotton. In cages supplied with cotton, sunflower, giant ragweed, Johnson, and other grasses, *M. differentialis* would defoliate the cotton shoots before giving much attention to other foliage. Our cage records, however, supported by my field observations indicate that *M. differentialis* in its natural environments often feeds upon the coarse grasses and weeds listed above. Although often found roosting on the common ragweed (*Ambrosia psilostachya* DC.), in all of our tests *M. differentialis* refused to eat the leaves and flowers of this plant except when other plants were not available. While it feeds greedily on young corn and wheat, it fed sparingly or not at all on native grasses, Andropogon and tall grama grass, supplied in our cages.

Thelesperma trifidum (Poir.) Britton proved to be one of the chief host-plants of *Paraidemona punctata* (Stål). While several species of flowering plants may serve as suitable host-plants for this wingless acridian it is definitely a selective feeder. In the fields optimum numbers are associated with patches of Thelesperma, *Gaillardia pulchella* Foug., and Plantago. This small yellow grasshopper is widely distributed in north central Texas. In optimum habitats it reaches swarming (Isely 1937, p. 334) numbers during June. While occasional specimens are encountered even in August, large numbers disappear early with the fading of Thelesperma and Gaillardia. Just how one may misjudge a possible host-plant is shown by my field notes of June 6, 1932. *P. punctata* was swarming in an abandoned "shell rock," marl field overgrown with what appeared to be a pure stand of *Croton monanthogynus* Michx. On this field evidence I assumed that this croton was the host-plant of *P. punctata.* In later cage studies *P. punctata* refused to eat Croton.

Campylacantha olivacea olivacea Sc. is of special interest in its selective feeding. *Ambrosia psilostachya* DC., its host-plant, was refused or eaten sparingly by other species tested in our cages. As already indicated in the discussions of Figure 5, *C. o. olivacea* is primarily a flower and fruit feeder.

Two species that have received considerable attention in the matter of their food preferences belong to the genus Hesperotettix. Field workers frequently report these two species associated in the same habitat. Field observations and cage testing, however, point to *Amphiachyris dracunculoides* (DC.) Nutt. as the host-plant of *Hesperotettix viridis viridis* (Thos.), and to *Helianthus annuus* L. as the primary host of *Hesperotettix speciosus* (Sc.). In my enclosed experimental garden I observed in the late spring and early summer of 1937 a small colony of *H. speciosus* develop through an entire series of instars in association with a single large sunflower plant. They roosted in the axils of the leaves and on the stems. The fuzzy silver white

juveniles harmonize very well with the woolly white stems of the sunflower.

Melanoplus texanus (Sc.) received a great deal of experimental attention in our food preference studies. While it would eat under starvation pressure the foliage of a number of plants, *Gaillardia pulchella* Foug. and Plantago proved to be the choices among the food plants offered. Field checks show that Gaillardia communities afford maximum numbers of this common short-winged June acridian.

Melanoplus plebejus (Stål) was the only representative of the sub-family Cyrtacanthacrinae which definitely preferred grasses. This species was not very extensively studied. Its feeding behavior is indicated in the discussion in connection with Figure 5.

Melanoplus flabellatus Sc., a very wide ranging species, undoubtedly has a larger number of suitable host-plants than our cage studies suggest. Tests point to *Engelmannia pinnatifida* T. & G. as one of the possible host-plants of this species.

Melanoplus ponderosus ponderosus Sc. has already been mentioned in connection with Figure 5. This species shows a marked preference for flowers and fruit as food.

Two species that were persistently studied in cages were *Melanoplus confusus* Sc. and *Melanoplus impiger* Sc. The former is a widely distributed spring species but not especially abundant in any given habitat locally. In tests no plant was found which was especially selected as food by this species (Tables 3 & 5). *M. impiger* also gave difficulty for two seasons. Field observations and cage tests in 1937, however, pointed to the *Rudbeckia hirta* L., as the host-plant for this species.

Dactylotum pictum (Thos.), sometimes called the "barber pole grasshopper," is a selective feeder. In field checking it was only found as an occasional specimen unless definitely associated with its primary host-plant, *Baccharis texana* (T. & G.) Gray. In addition to the species shown in Table 3 several other spine-breasted grasshoppers were checked for food preferences for short periods in our cages.

Hypochlora alba (Dodge), as various field workers have suggested, is definitely associated with the white sage, *Artemisia ludoviciana* Nutt., as its specific host-plant. Cage tests show that *H. alba* will, however, live for ten days supplied with broomweed and sunflower.

Melanoplus discolor (Sc.) in cages showed a definite preference for *Salvia farinaceae* Benth. This small short-winged grasshopper has a wide distribution, especially in prairie pastures, and may have other food preferences.

The food preferences of *Melanoplus keeleri keeleri* (Thos.), and *Melanoplus mexicanus mexicanus* (Sauss.), were especially studied by one of my students, Miss Frances Kelly, in the Trinity University Biological Laboratory (1935-1936). Miss Kelly's unpublished paper reports that *M. k.*

keeleri feeds upon several dicotyledons. *Parthenium hysterophorus* L., and giant ragweed (*Ambrosia aptera* DC.), are named as host-plants. *M. m. mexicanus* has been thoroughly studied by economic entomologists. In our cages *M. m. mexicanus* selected rather widely among monocotyledons and dicotyledons showing a definite preference for crop plants.

Melanoplus scudderi latus Morse, a late fall, timber margin species, selected the foliage of the giant ragweed, sunflower, and Parthenium as food. Among the crop plants, alfalfa (*Medicago sativa* L.) was eagerly eaten.

ADDITIONAL PLANTS OFFERED AS FOOD

As already indicated the plants listed in Tables 1-3 represent plant species found to be acceptable as food to one or more of the acridian species being checked for food preferences. Furthermore, with the exception of the crop plants these plants belonged to the flora of the habitats from which the acridians were collected.

The plants listed, which follow, are made up chiefly of two different groups of plants, as far as their distribution is concerned. In the first group belong species of plants represented by large numbers of individuals in the flora of optimum habitats of the acridians being studied. These plants, however, were for the most part refused in our cages as food or eaten sparingly. In the second group belong chiefly pest-weeds and pest-grasses found in gardens, fields, and vacant lots. To the second group may be added a few of the common garden and crop plants. The plants of the second group were handy for use as fresh green foods or at times were used as emergency foods when other vegetation from the flora of optimum acridian habitats was not available. The chief interest in the latter group of plants lies in the fact that if eaten they serve to show the adaptability of grasshoppers to plant foods which are not in their regular menu. Group one plants are as follows:

Meriolix spinulosa (T. & G.) Heller; *Megapterium missouriense* (Sims) Spach., Giant Evening Primrose; *Daucus pusillus* Michx., Wild Carrot; *Stillingia sylvatica* L.; *Paronychia scoparia* Small, Whisk-broom; *Verbena bipinnatifida* Nutt., Wild Verbena; *Valerianella amarella* Krok., Geometric chickweed; *Opuntia humifusa* Raf., Cactus; *Penstemon cobaea* Nutt.; *Brauneria angustifolia* (D. C. Heller), Pink Cone Flower.

To the second group belong the following: *Hieracium longipilum* Torr., Wild lettuce; *Linum lewisii* Pursh., Blue Flax; *Lupinus texensis* Hook, Texas Blue-bonnet; *Sonchus asper* (L.) Hill, Sow-thistle; *Oxalis* sp.; *Melilotus alba* Desv., Sweet clover; *Carduus virginiana* L., Common Thistle; *Ratibida columnaris* (Sims) D. Don, Niggerhead. In this plant series wild lettuce and sow-thistle were freely eaten by several acridian species.

Several grasses were eagerly eaten, often in preference to grasses from optimum acridian habitats. Among these grasses were the following: *Poa*

annua L., Annual bluegrass; *Hordeum pusillum* Nutt., Little barley; *Limnodea arkansana* (Nutt.) L. H. Dewey; *Digitaria sanguinalis* (L.) Scop.; *Echinochloa colonum* (L.) Link, Jungle rice.

The repeated selection by grasshoppers of foods not in their normal menu emphasizes the complexity of the environmental factors which control their living conditions. The ever present effectiveness of the law of the minimum (Hesse 1937, p. 21) must serve to limit certain acridians to environments where even preferred foods may not be available. Under these conditions, second choice foods with proper diet prerequisites have become established as host-plants.

In this argument the fact must not be overlooked that plants eaten freely may not always contain the necessary diet requirements for species maintenance (Hodge 1933; Carothers 1923).

STARVATION EXPERIMENTS

Cage studies dealing with the reactions of Acrididae to a wide variety of plant foods clearly demonstrated that at least 30 of the forty species checked should be classed as selective feeders. In other words, the number of palatable food plants for most species was found to be limited. To further examine the current biological as well as layman's theory that grasshoppers "eat everything green" and are both "*polyphagous* and *omnivorous*," a series of unpalatable food experiments was devised. The name starvation experiments has been applied to these tests since it was soon found that many species of grasshoppers would die in the absence of their specific host-plants, even when an abundance of fresh green vegetation, acceptable to other acridian species, was provided in their cages. The routine of these experiments was varied. The details of the tests are briefly summarized in the following paragraphs and tables.

Experiment 1—Two regulation cages (Fig. 1) were used. The food for Cage 1 represented four pasture grasses from the optimum habitats of the grasshopper species being tested:

Andropogon saccharoides Swartz
Stipa leucotricha Trin. and Rupr.
Aristida purpurea Nutt.
Cynodon dactylon (L.) Pers.

The food for Cage 2 was selected from abundant early June forbs also found in the optimum habitats of these species. The following forbs were used:

Gaillardia pulchella Foug.
Plantago sp.
Thelesperma trifidum (Poir.) Britton
Evax multicaulis DC.

On June 3, 1937 thirty specimens of four common June acridians were placed in each of the cages:

	I. Male	I. Female	II. Male	II. Female
Melanoplus confusus Sc.	4	4	4	4
Melanoplus texanus (Sc.)	4	4	4	4
Paraidemona punctata (Stål)	4	4	4	4
Acrolophitus variegatus (Thos.)	3	3	3	3

TABLE 4. STARVATION EXPERIMENT NO. 1
Longevity of four different acridian species supplied with:
I. Grasses, II. Forbs

Date 1937	Acridian Species	Cage 1. Grasses Numbers			Cage 2. Forbs Numbers		
		Male	Female	Dead	Male	Female	Dead
June 3	*M. confusus*	4	4	0	4	4	0
	M. texanus	4	4	0	4	4	0
	P. punctata	4	4	0	4	4	0
	A. variegatus	3	3	0	3	3	0
June 5	*M. confusus*	4	4	0	3	4	1
	M. texanus	2	4	2	4	4	0
	P. punctata	1	2	5	4	3	1
	A. variegatus	1	2	3	3	2	1
June 8	*M. confusus*	3	2	2	2	3	2
	M. texanus	1	4	1	4	3	1
	P. punctata	0	1	2	4	3	0
	A. variegatus	0	1	2	3	2	0
June 12	*M. confusus*	0	1	5	1	1	3
	M. texanus	0	2	3	3	3	1
	P. punctata	0	0	1	4	3	0
	A. variegatus	0	0	1	3	2	0
June 16	*M. confusus*	0	0	1	1	1	0
	M. texanus	0	0	2	3	3	0
	P. punctata	0	0	0	4	2	1
	A. variegatus	0	0	0	3	2	0
	Totals	All dead		30	19 Alive		11 Dead

The results in Table 4 are positive. In Cage 1 the thirty acridians belonging to four different species were supplied daily with fresh grasses representing three of the dominant native grasses of the grand prairies and naturalized Bermuda grass. The record shows that at the close of the ninth day twenty-seven specimens were dead in Cage 1 and only three individuals remained. At the close of the thirteenth day the last three Cage 1 grasshoppers died. It is obvious that these species starved with a fresh supply of green grass as food.

In Cage 2 the acridians were supplied with forbs. In the case of three species the forbs used had been designated in Tables 1-3 as their host-plants.

In the case of *Melanoplus confusus* a specific host-plant had not been fully determined. At the close of the thirteenth day, eleven of the Cage 2 specimens were dead. Six of these belonged to the species *Melanoplus confusus.*

Experiment 2—The acridian species used in this test were chiefly grass feeders. (See Tables 1-3). When available only males were used. In several cases the full number of males was not available, and females were substituted. *Melanoplus differentialis* (Thos.) was introduced into this series for possible comparative data that might come from a study of its feeding behavior in association with the grass feeders. The foods for Cage 1 were three grasses:

Andropogon saccharoides Swartz—(Beard grass)
Sporobolus heterolepis A. Gray—(Dropseed)
Sorghum halepense (L.) Pers.—(Johnson grass).

In Cage 2 only forbs were supplied as food. These were selected from among the host-plants of other August acridians (Table 6). These broad-leaved flowering plants were to be found in the fields as mixed weeds along with the grasses used in Cage 1. The forbs used in Cage 2 were as follows:

Amphiachyris dracunculoides (DC.) Nutt.—(Broomweed)
Ambrosia psilostachya DC.—(Common ragweed)
Houstonia angustifolia Michx.—(Houstonia)
Artemisia ludoviciana Nutt.—(White sage)

The Houstonia was used in the tests for the first two days. After that white sage was substituted.

This is one of the most spectacular experiments of the entire series. The results are so striking that comment is hardly necessary.

The first three species listed in Cage 2, Table 5, are exclusive grass feeders and all Acridinae. The record shows that these succumb quickly in the absence of grasses from their menu. Several specimens of *Chortophaga viridifasciata* and *Encoptolopus sordidus costalis* survived a few days longer, but these also starved in the presence of an abundance of fresh dicotyledonous food. At the close of the first week only nine specimens remained alive in Cage 2. Five of the nine belong to the species *Melanoplus differentialis* and three to *Geneotettix deorum.* The record of this experiment seems to suggest that *G. deorum* does not depend wholly on grasses for its diet. The versatility and adaptability of *M. differentialis* to maintain itself on plant foods not belonging to its first choices are noteworthy. All ten specimens of *M. differentialis* in Cages 1 and 2, (Table 5) were alive and apparently in good physical condition at the close of the experiment, September 1, eight days after its beginning. This marked adaptability of this pest species may largely explain its destructive propensities.

The Cage 1 record is self-explanatory. All the grass feeders show a good average vitality with a fresh supply of their grass diet available.

TABLE 5. STARVATION EXPERIMENT No. 2
Longevity of grass feeders when supplied with a variety of forbs from among the host-plants of other acridians. The pest grasshopper, *M. differentialis*, represents a polyphagous species

Date 1937	Acridian Species	Cage 1. Grasses Numbers		Cage 2. Forbs Numbers	
		Alive	Dead	Alive	Dead
August 23	*S. admirabilis*	5	0	5	0
	M. maculipennis	5	0	5	0
	M. neomexicana	5	0	5	0
	C. viridifasciata	5	0	5	0
	E. s. costalis	5	0	5	0
	G. deorum	5	0	5	0
	M. differentialis	5	0	5	0
August 25	*S. admirabilis*	5	0	3	2
	M. maculipennis	4	1	1	4
	M. neomexicana	5	0	4	1
	C. viridifasciata	5	0	5	0
	E. s. costalis	5	0	5	0
	G. deorum	5	0	4	1
	M. differentialis	5	0	5	0
August 26	*S. admirabilis*	5	0	0	5
	M. maculipennis	4	0	0	4
	M. neomexicana	4	1	0	5
	C. viridifasciata	5	0	3	2
	E. s. costalis	5	0	5	0
	G. deorum	4	1	3	2
	M. differentialis	5	0	5	0
August 28	*S. admirabilis*	5	0	0	0
	M. maculipennis	4	0	0	0
	M. neomexicana	4	0	0	0
	C. viridifasciata	5	0	2	1
	E. s. costalis	5	0	3	2
	G. deorum	4	0	3	0
	M. differentialis	5	0	5	0
August 30	*S. admirabilis*	5	0	0	0
	M. maculipennis	4	0	0	0
	M. neomexicana	4	0	0	0
	C. viridifasciata	5	0	0	0
	E. s. costalis	5	0	1	2
	G. deorum	4	0	3	0
	M. differentialis	5	0	5	0
September 1	*S. admirabilis*	4	1	0	0
	M. maculipennis	4	0	0	0
	M. neomexicana	4	0	0	0
	C. viridifasciata	5	0	0	0
	E. s. costalis	5	0	0	1
	G. deorum	4	0	3	0
	M. differentialis	5	0	5	0
	Totals	31 Alive	4 Dead	8 Alive	27 Dead

The results of Experiments 1 and 2, Tables 4 and 5, *should explode the dictum that grasshoppers "eat everything green."* It is evident that nine of

the eleven species tested in these experiments will starve in the presence of abundant vegetation representing host-plant selections of other acridian species. It is noteworthy that this list of nine contains representative species from all three of the major North American sub-families of the Acrididae.

Experiment 3—The acridian species used in Experiment 3 feed chiefly on broad-leaved plants. Eight species were used:

Hesperotettix viridis viridis (Thos.)
Hesperotettix viridis pratensis (Sc.)
Hesperotettix speciosus (Sc.)
Melanoplus plebejus (Stål)

Hypochlora alba (Dodge)
Campylacantha olivacea olivacea Sc.
Trimerotropis pistrinaria Sauss.
Hadrotettix trifasciatus (Say)

At first only two cages were arranged. Forty specimens, five individuals of each species were put in each cage. The plant materials in Cage 1 were arranged as follows:

Amphiachyris dracunculoides (DC.) Nutt................................Broomweed
Solidago petiolaris Ait..Goldenrod
Helianthus annuus ....Sunflower
Andropogon saccharoides Swartz..Beard grass

In Cage 2 the following plants were supplied:

Artemisia ludoviciana Nutt...White Sage
Ambrosia psilostachya DC..Common Ragweed
Hymenopappus corymbosus T. & G.......................................Hymenopappus
Asclepiodora decumbens (Nutt.) A. Gray......................................Milkweed

The plants in Cage 1 consisted of the host-plants of the first four species of acridians. The Cage 2 plants consisted of the host-plants of the last four species. Six of the plants used are shown in Table 3 as the first choices of the species concerned. *H. v. pratensis* was not among the species shown in Table 3. Its host-plant, however, *Solidago petiolaris* Ait., was among the food plants in Cage 1. In the case of *M. plebejus*, instead of Johnson grass beard grass was supplied.

Experiment 3 was started on August 23. On August 28 it was decided to introduce a third cage using forty specimens belonging to the same species as in Cages 1 and 2. Cage 3 was to be supplied with grasses for food but no forbs. The grasses selected were acceptable food plants for the grass feeders tested in Experiment 2, Table 5. The grasses supplied were as follows:

Andropogon saccharoides Swartz—Beard Grass
Sorghum halepense (L.) Pers.—Johnson Grass
Sporobolus heterolepis A. Gray—Dropseed

On September 1 we replaced the Johnson grass with
Andropogon furcatus Muhl—Bluejoint Turkeyfoot.

The results of this experiment are shown in Table 6.

Table 6. Starvation Experiment No. 3
Adaptability of Eight Acridian Species to Three Different Plant Menus

Date 1937	Acridian Species	Cage 1. Host-plants of H.v.v., H.p., H.s. and M.p. Numbers		Cage 2. Host-plants of H.a., C.o.o., T.p. and H.t. Numbers		Cage 3. Host-plants of grass feeders, Cage 1, Exp. 2. Numbers	
		Alive	Dead	Alive	Dead	Alive	Dead
Aug. 23	*H. viridis*	5	0	5	0	Not started	
	H. pratensis	5	0	5	0		
	H. speciosus	5	0	5	0		
	M. plebejus	5	0	5	0		
	H. alba	5	0	5	0		
	C. olivacea	5	0	5	0		
	T. pistrinaria	5	0	5	0		
	H. trifasciatus	5	0	5	0		
Aug. 25	*H. viridis*	5	0	4	1	Not started	
	H. pratensis	5	0	3	2		
	H. speciosus	5	0	4	1		
	M. plebejus	5	0	4	1		
	H. alba	5	0	4	1		
	C. olivacea	4	1	4	1		
	T. pistrinaria	3	2	4	1		
	H. trifasciatus	4	1	5	0	Started Aug. 28	
Aug. 27	*H. viridis*	5	0	2	2	5	0
	H. pratensis	5	0	0	3	5	0
	H. speciosus	5	0	0	3	5	0
	M. plebejus	5	0	4	0	5	0
	H. alba	5	0	4	0	5	0
	C. olivacea	4	0	4	0	5	0
	T. pistrinaria	1	2	4	0	5	0
	H. trifasciatus	2	2	4	1	5	0
Aug. 30	*H. viridis*	5	0	1	1	5	0
	H. pratensis	5	0	0	0	1	4
	H. speciosus	5	0	4	0	3	2
	M. plebejus	5	0	4	0	5	0
	H. alba	4	1	4	0	5	0
	C. olivacea	2	2	4	0	3	2
	T. pistrinaria	0	1	3	1	5	0
	H. trifasciatus	1	1	3	1	5	0
Sept. 1	*H. viridis*	5	0	0	1	5	0
	H. pratensis	5	0	0	0	1	0
	H. speciosus	5	0	4	0	2	1
	M. plebejus	5	0	4	0	5	0
	H. alba	1	1	4	0	3	2
	C. olivacea	2	0	4	0	3	0
	T. pistrinaria	0	0	3	0	5	0
	H. trifasciatus	0	1	4	0	4	1
Sept. 3	*H. viridis*	5	0	0	0	0	5
	H. pratensis	5	0	0	0	0	1
	H. speciosus	5	0	4	0	0	2
	M. plebejus	5	0	4	0	4	1
	H. alba	0	1	4	0	3	0
	C. olivacea	3	0	4	0	0	3
	T. pistrinaria	0	0	3	0	5	0
	H. trifasciatus	0	0	4	0	3	1
		Alive	Dead	Alive	Dead	Alive	Dead
Totals	Upper 4 species	20	0	8	12	4	16
	Lower 4 species	3	17	15	5	11	9

Cages 1 and 2 were closed out September 3. Cage 3 was continued until September 10. At that time there were still five live grasshoppers in Cage 3. These were: *H. trifasciatus* 3, *T. pistrinaria* 1, and *M. plebejus* 1. It was evident that even these survivors were not thriving on the prairie grass menus supplied in Cage 3.

The results of Experiment 3 are shown in the totals of Table 6. In Cage 1 all the grasshoppers belonging to the upper four of the eight species being tested were alive. These had been supplied with their host-plants as food. Only three grasshoppers belonging to the lower four species were alive in Cage 1.

In Cage 2 the results were not quite as definite. Fifteen grasshoppers were alive to represent the lower four species and four each of *H. speciosus* and *M. plebejus.* Cage 3 results, however, show that even *H. speciosus* and *M. plebejus* have specific food requirements.

In Experiment 3 the same facts stand out which were apparent in Experiments 1 and 2, Tables 4 and 5. Many species of grasshoppers are selective feeders and will soon die in the presence of abundant fresh vegetation if they are deprived of their host-plants. The case of *Campylacantha olivacea olivacea* is cleared up if we compare Table 3 and Figure 5. While the chief food of this species is made up of the foliage of the common ragweed their feeding on the flowers of Amphiachyris explains their longevity in this experiment. The hardiness of *Hypochlora alba* came as a surprise. *Melanoplus plebejus* and *Hesperotettix speciosus* in Cages 1 and 2 are evidently more adaptable to the forbs foods supplied than are the other species. In Cage 3, however, with a grass diet a zero is found in the alive column for *H. speciosus* at the close of the tenth day. In Cage 3 *Trimerotropis pistrinaria* stands out as having five survivors on the sixth day with a grass diet. Fasting tests show, however, that even in warm weather certain species from xeric habitats will live without food or water for a week. Mature females usually live longer than males in starvation tests.

STARVATION IN ABSENCE OF FOOD

Under normal north central Texas summer temperatures and the consequent high metabolism, how long can a grasshopper live without food? There are, no doubt, individual differences as well as species differences. In order to make a further trial a no-food experiment was set up on September 1, 1937.

Vigorous pairs of all of the fifteen species used in Experiments 2 and 3 (Table 5 and 6) were placed in a cage (Fig. 1) without food. In addition to these, pairs of the following species were added: *Melanoplus discolor* (Sc.), *M. k. keeleri* (Thos.), *M. bispinosus* Sc., and *M. p. ponderosus* Sc., making 19 pairs or 38 specimens in all. The empty soil pans were filled with clean sand; water was supplied daily by wetting the sand and the sides of the cage. The temperature during the period the experiment was in progress, September 1-10, ranged from a minimum of 68°F to a maximum of

96°F. All daily maximum records for the period were between 92°-96°F. Minimum night temperatures were between 68°-74°F.

On September 3, two days after the experiment started, 9 specimens were dead; 6 males and 3 females. The dead specimens were always removed as rapidly as seen, for it is well known that grasshoppers will frequently feed on dead ones. However, I have not observed predacious behavior on the part of acridians, although starving grasshoppers will eat off the antennae of those that are dying or nearly dead.

Specimens of other species died gradually until on September 8, after one week in the "no-food" cage, 8 live grasshoppers remained. The species and sexes were as follows: females, one each, *H. trifasciatus, H. v. viridis,* and *Hypochlora alba;* one male, *M. differentialis.* For two species, *M. bispinosus* and *M. p. ponderosus,* both males and females were still alive. With the exception of the pair of *M. p. ponderosus* the remaining specimens were dead by September 9. This hardy species in repeated tests lived from 12 to 14 days in cages supplied with water but no food.

In experiments where grasshoppers were supplied with unpalatable food in the cages, as well as in this experiment without food, the absence of feces is noticeable. From the taxonomic viewpoint longevity without food or with unpalatable food shows that the Cyrtacanthacrinae have the greatest powers of survival. The Oedipodinae are second, and the Acridinae are the least hardy among the sub-families studied.

Omnivorous Feeders

The idea that grasshoppers are to an extent omnivorous feeders is supported in part by the fact that dead grasshoppers were often eaten in cages. As I have already indicated, acridians show no marked predacious tendencies. In cages where there are many specimens, dead grasshoppers are usually partly eaten even when there is an abundance of palatable food. From the data at hand in these starvation tests, however, this tendency to feed upon dead grasshoppers appears to be of significance only in the temporary maintenance of starvation survivors at times of food shortage until more desirable food is found.

FOOD PREFERENCES ANALYZED

An analysis of the feeding behavior of the forty acridian species experimentally tested shows that exactly twenty of the forty species were primarily grass feeders. The twenty other species chose their host-plants from among the forbs or the broad-leaved flowering plants. These food preferences grouped by acridian sub-families are as follows:

Sub-Family	*Grasses*	*Forbs*
Acridinae	9	1
Oedipodinae	10	2
Batrachotetriginae	0	1
Cyrtacanthacrinae	1	16
Totals	20	20

Grass eaters, while definitely restricted to grasses, selected their food as a rule rather freely from among several species when these were available.[15] However, certain of the grass species were not acceptable even to the grass eating grasshoppers.

The species showing marked preferences for forbs belong chiefly to the Cyrtacanthacrinae (spine-breasted grasshoppers). Nine of the sixteen species of the Cyrtacanthacrinae selected their food from among the Compositae. This fact is of interest from the evolutionary and taxonomic viewpoints when it is noted that what is believed to be the most recent sub-family phylogenetically selects its host-plants from among the most recent phylogenetic family of the angiosperms.

Cage tests clearly show a correlation among the grass feeders with grass habits of growth. This correlation suggests shelter and protection going hand in hand with plants needed for food. The slender bodied Mermiriae and Syrbulae: *Mermiria maculipennis maculipennis* Bruner, *M. bivittata* (Serville), *M. neomexicana* (Thos.), *Syrbula admirabilis* Uhler, and *S. fuscovittata* (Thos.) find their habitats among the Andropogons, Sporobolus, and the tall grama grasses. *Geneotettix deorum* (Sc.), *Mesochloa abortiva* Bruner, *Opeia obscura* (Thos.), *Orphulella speciosa* (Sc.), and *Trachyrhachis kiowa fuscifrons* (Stål), small, usually somewhat flattened acridians frequent low, mat-like grasses, especially buffalo and Bermuda grass.

East and north certain of these short grass species will be found associated with the blue grasses (Poas). *Chortophaga viridifasciata* (DeGeer), *Arphia simplex* Sc., *Encoptolophus sordidus costalis* (Sc.), and *Dichromorpha viridis* (Sc.) are more frequently associated with the lush grasses of the streams and timber margins.

There are few acridians that are so closely associated with their host-plants as to be found exclusively on a single plant species in field observations. This association involves the use of plants not only as food but for roosting among the shoots and on the branches. *Hypochloa alba* (Dodge), well known to all field students of grasshoppers of the great plains, illustrates in a striking way this behavior in its close association with *Artemisia ludoviciana* Nutt. As far as my field studies are concerned, I have never taken *H. alba* except in the immediate vicinity of its host-plant. In cage tests, however, under starvation pressure it fed on other plants. While not as highly selective and as clean-cut in their natural habitat relationships as *H. alba*, I have found very similar host-plant relationship on the part of *Dactylotum pictum* (Thos.), *Hesperotettix speciosus* (Sc.), *Hesperotettix viridis viridis* (Thos.), *Hesperotettix viridis pratensis* (Sc.), and *Campylacantha olivacea olivacea* Sc. These roost upon and feed upon the foliage

[15] Criddle (1933 a, p. 480) in his study of food preferences of Manitoba grasshoppers found three species, *Opeia obscura* Thos., *Metator pardelinus* Sauss., *Melanoplus o. occidentalis* Thos., selecting *Agropyron smithii* Rydb. as their host-plant. One of these species, *Opeia obscura* Thos., is occasionally represented in the acridian fauna (Isely 1935, p. 43) of north central Texas.

and in some cases the flowers and fruits of the host-plants. Among the Acridinae *Acrolophitus variegatus* (Thos.) is restricted to a specific host-plant, *Evax multicaulis* DC. Certain other species while definitely selecting certain specific plants for food differ in their roosting behavior. These species move about more freely and do not cling as tenaciously to their host-plants. In this list are *Paraidemona punctata* (Stål), *Melanoplus texanus* (Sc.), and *Brachystola magna* (Girard). These species do not mark out their host-plants as definitely as the acridians noted above. When not feeding they are as likely to be found on the ground or other low vegetation as upon their host-plants. Still other species like *Melanoplus differentialis* (Thos.) and *Melanoplus ponderosus ponderosus* Sc. roost frequently upon plants that are not used for food.

Accidental association of acridians and plants have often led field observers to suspect host-plant relationships. Cage studies, however, definitely show that roosting preferences often have no relation to food preferences. For example cage studies show that certain grass feeders (*Syrbula admirabilis* Uhler) roosting on the common ragweed (*Ambrosia psilostachya* DC.) starve if forced to use this plant as food.

The results of the starvation experiments summarized in Tables 4-6 are obvious. Since specific plant species are essential as food for certain acridians. An optimum acridian habitat must be favorable not only to the acridian species but also to the host-plant species.

The seasonal passing of a plant species, the dying of certain plants on account of drouth, or over-grazing in certain pastures will be followed immediately by the dying of the acridian species using these plants for food. Frequently, in a nearby pasture under conditions more favorable to the host-plants, the acridians will continue to thrive, although they have disappeared in the other areas as indicated above. The temporary change under starvation pressure to other plants for food may occur, but for optimum nutrition and reproductive needs the right kind of food is of primary importance. This necessary diet requirement can only be satisfied where specific plants are a part of the flora of the habitat of the acridian species. These facts are further emphasized by the researches of Carothers, Criddle, and Hodges previously cited.

Finally, these food preference and starvation studies indicate that 30 of the 40 species studied are essentially oligophagous. Four species approach monophagy, only two are typically polyphagous. The four species that come the nearest to monophagy in their field behavior are *H. alba, D. pictum, A. variegatus,* and *H. v. viridis.* To the four may be added *H. v. pratensis,* not included in the forty listed in connection with the tables. The feeding behavior under natural conditions of *H. v. pratensis* is different from the feeding behavior of *H. v. viridis.* In cages *H. v. pratensis* fed on broomweed, the chief host-plant in our area of *H. v. viridis.* In field checking,

however, it was found that *H. v. pratensis* is closely associated with *Solidago petiolaris* Ait. Further study may place a few of the 30 oligophagous species in the polyphagous group. In the main, however, it may be emphasized that my experiments indicate that north central Texas acridians in general require specific foods for their species maintenance.

SOIL CHOICES FOR OVIPOSITION

SOIL RELATIONS

In the literature at hand[16] I find only two references suggesting experimental study of soil choices for oviposition. McClung (1899, p. 21) made such a test with *Melanoplus differentialis* (Thos.). His results show selective behavior on the part of this species. Uvarov (1928, p. 57) suggests the use of "special cages each containing several different samples of soil."

In a recent paper Shotwell (1935, p. 486) gives descriptions of egg laying sites as usually selected in nature by a few of the best known economic species. Criddle (1918; 1933a, p. 482) has observed and described the egg laying behavior in the field of several Manitoba species. He discusses soil choices for egg laying under natural conditions.

Economic entomologists in describing egg laying sites of pest species usually emphasize the importance of unplowed field margins, fence rows, road sites, and waste fields (soil structure) as possible concentration areas for egg laying. Topography as related to drainage is considered significant. Vegetation affording roots and grass crowns is also pointed out as attracting certain species in selecting sites for egg laying.

That there is a clean-cut correlation between grasshoppers and different soils appears to be the general conclusion of critical field students of these insects. In a recent paper (Isely 1937, p. 325) attention is called to the close interrelations of acridians and soils.

Is this definite association primary and determined by the reactions of acridians to soil structure, texture, moisture, pH, or some other soil factors; or is it secondary and determined by the presence of plants necessary in diet, which are in turn definitely soil related? Certain species, *Spharagemon collare cristatum* (Sc.) and *Melanoplus impiger* Sc., reach their greatest numbers only in light sandy soil habitats. A few other well known examples are: alluvial soil species, *Melanoplus differentialis* (Thos.), and *Dissosteira carolina* (L.); eroded soil species, *Trimerotropis pistrinaria* Sauss.; calcareous soil species, *Xanthippus corallipes pantherinus* (Sc.).

Dissosteira carolina (L.) in north central Texas is definitely an alluvial soil grasshopper, never abundant but usually found in "first bottom" habitats. In Kansas (Sedgwick County) on account of its distribution the name "road duster" is generally applied to the Carolina grasshopper. In Colorado from 6000-8000 feet elevation (Boulder County) the abundance of *Dis-*

[16] There probably have been other experiments, but in the literature at hand this is the only reference given.

sosteira carolina (L.) is limited to miniature valleys among the rugged mountains. This highly adaptive species appears to vary its choice of habitat, although in the cases cited above wash soils are evidently selected for oviposition.

SOIL SELECTION EXPERIMENTS

The experimental set-up for our food preference testing gave fairly satisfactory results. To secure positive experimental data concerning soil choices for oviposition has proven thus far to be more difficult. Enough data have been secured, however, to emphasize the fact that Acrididae do react to soil differences and appear at times to choose certain types of soil for oviposition in preference to others.

Four hundred and nine egg pods were deposited by thirty-two different acridian species in soil pans in cages. The soils selected for oviposition by eighteen species depositing as many as six pods or more are shown in Table 7. A record of six pods may be suggestive of possible behavior but provides insufficient data for any final deductions.

Further facts concerning egg pods, egg packets, stoppers, and eggs are given in Table 9. The soil pans described in connection with Figure 1 were especially devised to test out acridian soil choices in oviposition. A diagram (Fig. 6) of the floor plan of the cage and the spaces occupied by the soil pans will help to explain the technique used in testing reactions of Acrididae to soils for egg laying.

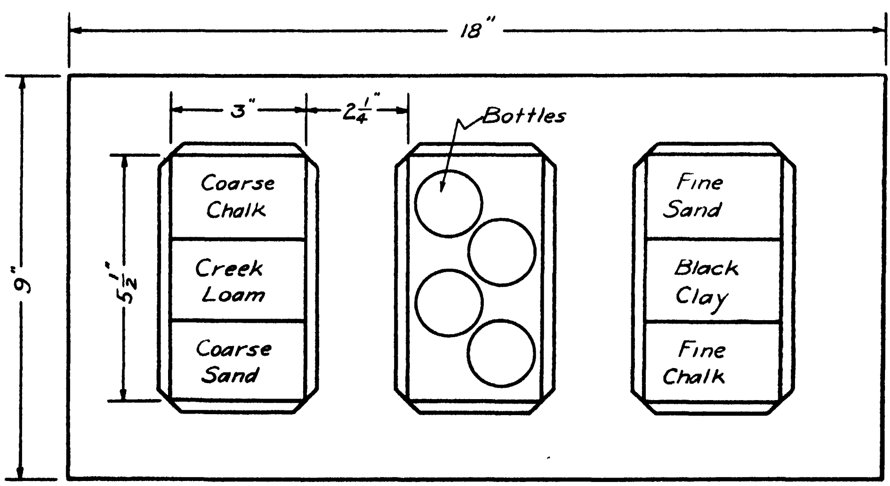

FIG. 6. A diagram of a cage floor (Fig. 1) showing soil compartments used for checking soil choices for oviposition. Five or six different kinds of soils were usually available. The female grasshoppers, after testing, selected from among these soils the particular sites for depositing their egg pods. Turf was sometimes substituted for one of the other soils. The bottles in the center soil pans were used to hold fresh plant shoots for food. Fig. 1 shows soil pans on top of the cage. Compartments and soils in these pans are also shown.

The different soils were secured from optimum habitats of the various species to be tested. Some of the common local soil types used were the following: (1) chalk or marl, the eroded sub-soils of Houston clay shallow phase areas; (2) creek loam, alluvial soils, a mixture of water-lain soils, silt and sand; (3) black clay soils representing the stiff Houston clay of the blackland prairies; (4) fine sand secured from the east Texas timbers or the Cahaba fine sands; (5) coarse sand; (6) sifted chalk or marl; (7) turf, small blocks or transplanted turf. Soil 6 was a fine grained calcareous soil with a structure similar to "fine sand" in 4. Soils 5 and 1 were also similar in structure, although very different in texture. Soils 6 and 7 were introduced late in this series of experiments and were not placed in the cages in the earlier tests which were used to check the reactions of grasshoppers to soils differing in texture, structure, and chemical composition. Soils 1-6 were bare soils and without vegetation. After various soils were placed in the several compartments of the soil pans they were thoroughly settled by wetting. The turf blocks of soil employed in a few of the experiments gave opportunity for selection of oviposition sites associated with vegetation.

ACRIDIAN SPECIES USED FOR OVIPOSITION EXPERIMENTS

Mature females secured directly from optimum habitats were used for oviposition experiments. As a rule from twenty to forty specimens, males and females in approximately equal numbers, were placed in a cage (Fig. 1). These cages were usually arranged with five or six different kinds of soils in the compartments of the soil boxes. The third soil pan was used to hold plant materials for food, and frequently one of the six smaller compartments was also used to hold plant materials. In addition the floor on the sides of the cage (Fig. 1) was used for bottles to hold food materials. When the host-plants were known these, if available, were always supplied for food. It was found that the right kind of food is of primary importance in securing egg laying activity.

Since all of the species studied in Tables 7 and 9 have been listed with their full scientific names in connection with Tables 1-3, this detailed list is not repeated in connection with these tables.

A study of Table 7 suggests that many of the species tested preferred soils made up of fine particles for egg laying. It is noteworthy that after the sifted-chalk-marl was introduced (FiCh), that with one exception, this fine structured calcareous marl paralleled rather closely the fine arenaceous sand

[17] These soils are described in county and state soil surveys (Isely 1937, p. 321). Soil texture is best indicated by mechanical analysis.

Mechanical Analysis of Ellis County Soils as given by Bennett 1911, Soil Survey of Ellis County, Texas, U. S. Bur. Soils, 1-34

Type of Soil	Fine Gravel Per cent	Coarse Sand Per cent	Medium Sand Per cent	Fine Sand Per cent	Very fine Sand Per cent	Silt Per cent	Clay Per cent
Houston Black Clay	0.4	1.4	0.8	3.0	7.6	44.7	42.2
Houston Stony Clay	0.0	0.4	0.4	4 9	26.2	44.1	24.4
Trinity Clay	0.1	0.5	1.3	4.4	2.3	29.4	60.1
Bienville Fine Sand	0.0	1.0	12.3	76.4	5.0	2.7	2.5

Table 7. Soils Chosen for Oviposition

Column Headings:
Dates —Duration of tests.
I-XII —Months.
AvF —Average number females in cage.
Total Pods —Total egg pods.
Soils:
CoCh —Coarse Chalk or Marl.
CrLm —Creek Loam.
CoSd —Coarse Sand.
BlCl —Black Clay.
FiSd —Fine Sand.
FiCh —Sifted Fine Chalk.
Tf —Turf.
0-21 —Number of pods.
-- —Not used.

Arrangement of species in seasonal sequence of acridian egg laying
Number of Egg Pods Laid in Different Soils

Acridian Species	Dates 1936	AvF	CoCh	CrLm	CoSd	BlCl	FiSd	FiCh	Tf	Total Pods
M. confusus	V,4-31	24	3	9	5	4	16	--	--	37
A. simplex	VI,1-20	24	6	15	5	8	13	--	--	47
X. c. pantherinus	VI,1-VII,11	11	1	0	4	2	7	1	0	15
P. punctata	VI,1-22	40	13	8	21	3	18	--	--	63
M. texanus	VI,1-25	20	2	12	4	3	13	--	0	34
P. saussurei	VI,15-VII,18	10	0	1	1	0	4	2	0	8
S. c. cristatum	VI,20-30	19	0	3	1	0	7	5	--	16
H. v. viridis	VII,1-31	28	7	0	5	1	2	0	17	32
H. speciosus	VII,1-31	22	10	3	5	2	4	16	--	40
M. flabellatus	VII,1-16	6	2	1	4	1	0	0	--	8
D. pictum	VII,13-VIII,3	15	2	4	1	1	3	0	--	11
H. trifasciatus	VII,29-VIII,5	15	2	0	3	--	1	0	0	6
M. discolor	VIII,1-8	30	0	5	0	--	5	4	--	14
G. deorum	VIII,1-8	11	0	0	0	0	9	0	0	9
C. o. olivacea	IX,20-30	10	0	1	0	0	3	4	0	8
S. admirabilis	XI,1-28	6	0	4	0	0	3	0	--	7
M. k. keeleri	XI,1-30	10	0	2	0	5	15	2	--	24
M. m. mexicanus	XI,27-XII,4	4	--	--	--	3	3	3	--	9
Totals	....		48	68	59	33	126	37	17	388

in the number of times it was selected for oviposition. Four species (*S. c. cristatum, M. discolor, C. o. olivacea* and *M. m. mexicanus*) show this similarity in their reactions to soil structure and apparently disregard differences in the chemical composition of soils.

Soils made up of *fine particles* composed of fine sand, sifted-chalk-marl, and creek loam were selected for egg laying sites in preference to soils of *coarse materials* made up of gravel, broken rock, and stiff clay. These fine structured soils were chosen for egg laying sites in preference to the coarse structured soils in cage tests as follows:

Spharagemon collare cristatum (Sc.) selected soils made up of five particles for the laying of 16 pods out of a total of 17 egg pods, *Pardalophora saussurei* (Sc.) 7 times out of 8, *Geneotettix deorum* (Sc.) 9 times out of 9, *Melanoplus discolor* (Sc.) 14 times out of 14, *Melanoplus keeleri keeleri* (Thos.) 17 times out of 24, *Melanoplus confusus* Sc. 25 times out of 38, *Arphia simplex* Sc. 28 times out of 47, *Campylacantha olivacea olivacea* Sc. 7 times out of 8, *Syrbula admirabilis* Uhler 7 times out of 7.

For the nine species listed above these tests show that out of 172 egg pods deposited 130 were placed in soils made up of fine particles to 42 laid in soils made up chiefly of coarse materials or a ratio of 3 to 1 in favor of

soils composed of fine particles. Other reactions may be studied in Tables 7 and 8.

In comparison with these fairly uniform reactions to soil differences *Paraidemona punctata* (Stål) selected coarse structured soils 34 times in laying a total of 64 pods. *Hesperotettix speciosus* (Sc.) is of interest in selecting calcareous soils 26 times out of a total of 40 pods laid. *H. v. viridis* (Thos.) was the only species to select turf.

Herbert Knutson (1937), using a set-up similar to the ones summarized in Table 7, reports some interesting egg laying reactions for *Encoptolophus sordidis costalis* (Sc.). The black soil used by Knutson was secured from an optimum habitat of *E. s. costalis* and in terms of my classification would be similar to the black clay known to north central Texas soil students as Houston black waxy-clay. His experiments were carried on in the Biology Laboratory of Southern Methodist University and were continued for several months (October-May, 1936-1937). In the soil pans in his cages Knutson secured 204 egg pods of *E. s. costalis*. The data given in his thesis are as follows:[18]

Type of Soil	*Number of Eggs Pods Found*	*Percentage of Total Pods Laid*
Black	111	54.4%
Limestone	44	21.5%
Sand	20	9.8%
Red Sand	18	8.8%
Gravel	11	5.4%

In this study *E. s. costalis* selected calcareous soil 155 times in depositing 204 egg pods—a percentage of 75.9% of total pods laid.

In Figure 7 and Table 9 a few facts are given concerning egg pods and eggs. The female grasshopper first forms a cavity in the soil with her ovipositors in which the egg pod is deposited. These egg pods vary in size and form. As a rule, they correspond in size in a general way with the size of the grasshopper. As shown in Figure 7 the extremes in the size of the pods are represented by the large egg sacs of *Brachystola magna* (Girard) and *Pardalophora saussurei* (Sc.) on the one hand and the small egg pods of *Melanoplus flabellatus* Sc. and *Geneotettix deorum* (Sc.) on the other. The entire egg pod is usually made up of two parts, the egg packet proper and the stopper, a plug of mucilaginous material. In certain species *Hesperotettix viridis viridis* (Thos.) and *Hesperotettix speciosus* (Sc.), the stopper is represented by a thin layer of frothy material. In other cases, as *Spharagemon collare cristatum* (Sc.), the stopper represents four-fifths of the entire length of the pod. In Table 9 the average lengths of typical pods are indicated, as well as the relative lengths of the egg packet or mass of eggs as compared with the length of the stopper. The figures given for the average number of eggs in a packet represent the average number

[18] Mr. Knutson has kindly given permission to use his thesis data (unpublished). His cages (Fig. 1) and soil pans were the same as those used in the writer's experiments.

actually counted. The size of the eggs is surprisingly uniform. Measurements suggest 5 mm. as the average length of the eggs of many of the species studied. The eggs of the wingless species, *Paraidemona punctata* (Stål), represent the smallest size in individual eggs, averaging 4 mm. in length and 1 mm. in diameter and the eggs of *Brachystola magna* (Girard) the largest, averaging 6 mm. in length and 2 mm. in diameter.

The egg laying methods of grasshoppers are fully described in the literature and will not be further taken up at this time. Criddle (1933a) gives interesting details. The behavior activity of particular significance for this study was the testing of the soils by the females in selecting the particular

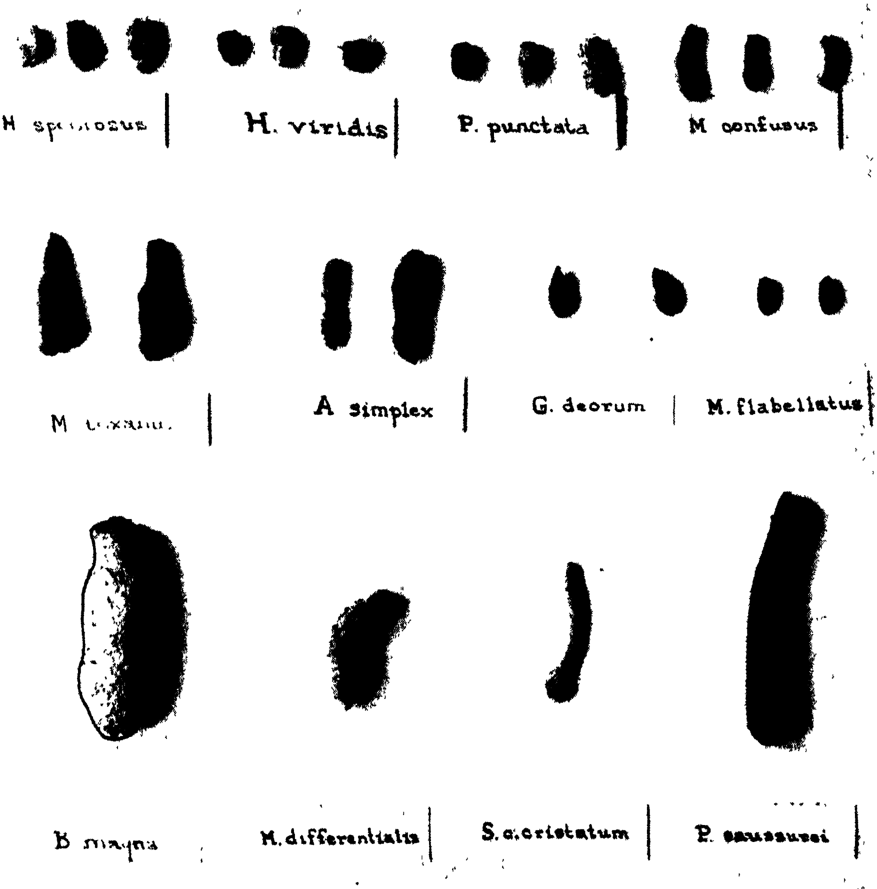

Fig. 7. Typical egg pods of 12 acridian species. For actual sizes (length and diameters) of pods see measurements given in Table 9. Pods with long stoppers are well represented by those of *S. c. cristatum* and *A. simplex*. Pods with relatively short stoppers are shown by *B. magna and M. texanus*. Stoppers were essentially absent in pods of *H. v. viridis*.

site for the oviposition of individual packets. In most instances it was observed that a number of tests are made by each individual female before the egg site was finally selected. Knutson (1937) suggests that the female tests the soil with her palps. The most evident testing, however, is done with the ovipositors. Frequently a female will burrow well into the ground and give up the particular site and test again and again before making a final selection. Since these preliminary egg cavities or drill holes are not closed by the female as are the cavities actually used for the egg pods, the soil in our soil pans was often pitted with drill holes. A comparison of the number of drill holes and the number of egg pods actually deposited by certain species is shown in Table 8.

TABLE 8. DRILL HOLES AND EGG PODS

Comparison of the numbers of drill holes and egg pods of *Syrbula admirabilis* Uhler and *Melanoplus keeleri keeleri* (Thos.).

COLUMN HEADINGS
Dates —Duration of tests
AvF —Average number females in cage
Totals —Total egg pods or drill holes

SOILS
CrCh —Coarse Chalk or Marl
CrLm —Creek Loam
CrSd —Coarse Sand
BlCl —Black Clay
FiSd —Fine Sand
FiCh —Sifted Fine Chalk

Acridian Species	Date 1935	AvF	CrCh	CrLm	CrSd	BlCl	FiSd	FiCh	Totals
S. admirabilis ..		6							
Drill Holes			0	6	4	6	5	0	21
Egg Packets	IX,23-XI,27		0	4	0	0	3	0	7
M. k. keeleri		10							
Drill Holes			0	0	4	25	20	3	52
Egg Packets	IX,23-XI,27		0	2	0	5	15	2	24

It will be noticed that *S. admirabilis* made 21 drill holes in four different soils (Table 8), but selected only two soils for the laying of seven egg pods. *M. k. keeleri* made 52 drill holes in selecting egg laying sites for the 24 pods which were later deposited. Fifteen of these pods were deposited in fine sand (Table 8).

The average number of eggs per packet of the species represented in Table 9 ranged from 4 to 30. *G. deorum* averaged four eggs per packet, and *B. magna* averaged 30. *X. c. pantherinus*, not shown in the table, averaged 87 eggs for the two packets dissected. This was the largest number for the 32 species studied. Economic entomologists give records of over 100 eggs per packet for *M. differentialis*.

Species associated with sandy soil egg laying sites in nature (*P. saussurei* and *S. c. cristatum*) show a much longer length for the stopper than those acridians which lay their eggs in clay soils. Turf layers (*H. v. viridis*) have the stopper reduced to the minimum.

EGG LAYING SITES—JUVENILES

Undoubtedly the breeding place is of primary significance in determining the habitat of an acridian species. Migratory grasshoppers, chiefly pest

TABLE 9. STRUCTURE OF EGG PODS AND EGGS

ABBREVIATIONS:

Pods. Exm. —Number of Pods Examined.
Av. Lg. of Pods. —Average Length of Pods.
Av. Lg. & Dm. Pkt. —Average Length and Diameter of Packets.
Av. Lg. & Dm. Stp. —Average Length and Diameter of Stopper.
No. Pods Dis. —Number Pods Dissected.
Av. Eggs in Pkt. —Average Number of Eggs in Packets.
Lg. & Dm. of Eggs —Length and Diameter of Eggs.
-- —Not determined.

All measurements of length and diameter are given in *millimeters*. Where two measurements are given in the same column the top one is for the length and the bottom one for the diameter.

Acridian Species	Pds. Exm.	Av. Lg. of Pods	Av. Lg. & Dm. Pkt.	Av. Lg. & Dm. Stp.	No. Pods Dis.	Av. Eggs in Pkt.	Lg. & Dm. of Eggs
A. simplex ..	11	30	16 5	14 --	6	25	5 1.5
P. punctata ..	17	12	9 6	3 5	6	9	4 1
M. texanus .	22	27	12 9	15	7	20	5 1.33
P. saussurei ..	3	54	15 --	39	1	28	5 1.75
S. c. cristatum .	8	34	8 5	26 3	5	17	5 1.3
H. v. viridis ...	8	8	7 7	1.5 4	5	12	4.5 1.3
H. speciosus ..	25	10	8.5 6	1.5 5	6	15	5 1.5
G. deorum	6	10	8 5	2 2	3	4	5 1.5
B. magna......	4	58	50 16	8 9	3	30	6 2
D. pictum	15	15	8 6	7 4	7	8	5 1.5

species, may move far away from the hatching site even in their nymphal stages.[19] After years of persistent field checking I am convinced that, as a rule, among our native species in north central Texas the entire series of juvenile instars is passed in close proximity to the place of hatching. The

[19] Criddle (1926, p. 505) uses the term larval for the first three instar stages and pupal for the fourth and fifth instars. Hebard usually employs the term juveniles for immature grasshoppers.

length of the juvenile period for most species which are hatched in the spring and summer is about five weeks, varying from 30 to 40 days. Life history cycles have been investigated by Carothers, 1923, p. 14; Criddle, 1933a, p. 475; and Shotwell, 1930, p. 20. In north central Texas we have ten species (Isely 1937) which are hatched in the late summer (September) and do not become adults until the last of the following March, or in April, or in May. In several of these species the winter is passed in the first instar, and the entire juvenile period occupies a span of seven to eight months.

HATCHING AREAS AS EVIDENCE OF SOIL CHOICES FOR OVIPOSITION

The grasshoppers that pass the winter as juveniles, as well as a number of other species are very distinctive even in their first instar stages. Such species may be studied as to their local distribution from the time of hatching to maturity through field observations. As already indicated the hatching centers of non-migratory species are essentially the same as the optimum habitats of the species concerned. There are several species, however, where the strong flying adults range rather widely from their egg laying sites. With these latter species the field study of early juveniles will help determine their egg laying soil relations.

Egg-pod surveys are employed by economic entomologists in locating the breeding centers of pest species. However, the so called "non-economic" species with which this paper is chiefly concerned, as a rule, do not occur in sufficient numbers to make the locating of egg pods practical in field surveys. The areas where juveniles are hatching or early instars are found can be used, however, to advantage in locating egg laying sites of these "non-economic" species. My most complete field data concern eight species: (1) Light sandy soil acridians, three species *Pardalophora saussurei* (Sc.) *Spharagemon collare cristatum* (Sc.), and *Melanoplus impiger* Sc. have been studied for several seasons in their early instar stages. These three species have been very abundant in favorable habitats, *M. impiger* even reaching numbers that might be designated as swarming (Isely 1935, p. 324). (2) Eroded sub-soil slope acridians, two species *Trimerotropis pistrinaria* Sauss., and *Acrolophitus variegatus* (Thos.) have been persistently studied. At their adult peak these species are common, but they do not become abundant even in their optimum habitats. However, these grasshoppers have been found in good numbers and have been continuously checked in field studies for the last three seasons (1935-37). As far as their *soil relations* are concerned, field evidence suggests that the chief index of the habitat of these two species in the blackland prairies of north central Texas is the eroded calcareous sub-soil slopes which mark their chosen optimum habitats. Their juveniles appear only where top soils have been washed away.

(3) Two other species similar in distribution to *A. variegatus* and *T. pistrinaria* are *Xanthippus corallipes pantherinus* (Sc.) and *Hadrotettix trifasciatus* (Say). Their hatching centers are on the tops of hills and ridges,

rather than on the sub-soil slopes. As a consequence the larger area available for suitable egg laying sites results in a wider distribution of the juveniles of these species. (4) Timber margin acridians, *Arphia simplex* Sc. in its adult activity has wide local distribution. Field records show early instar juveniles closely associated with timber margins. Since this species frequents blackland prairie, as well as sandy cross timber habitats, and is a general grass feeder, it seems obvious from its juvenile distribution that shelter is the controlling factor in its choice of egg laying sites rather than soil or specific food plants.

Egg laying sites of several other species have been checked, but not as thoroughly as for the eight species discussed above. These field data emphasize the importance of soil texture, structure, and composition as contributing factors in explaining local distribution of acridians.

GENERAL CONSIDERATIONS

ECONOMIC IMPORTANCE

In America the word grasshopper[20] has come to be synonymous with crop destruction. Only three of the forty species checked for their food preferences in these studies belong to "economic" species as they are usually listed by entomologists and experts in grasshopper control (Parker 1933, p. 3459). These species are *Melanoplus differentialis* (Thos.), *Melanoplus mexicanus mexicanus* (Sauss.), and *Brachystola magna* (Girard).[21] The 37 other acridian species discussed in connection with Tables 1-6 are usually classified by economic entomologists as non-economic and non-migratory grasshoppers. These acridians are, however, of biological interest, economically as well as ecologically. The grass feeders may exact their toll from overgrazed ranges and to this extent may damage the carrying capacity of the range for live stock. Weed-eating species, on the other hand, may be of value to agriculture and rightfully classed as beneficial (Gillette 1904, Ball 1936). All acridians certainly play an important part in biotic interrelationships. In cage tests *Melanoplus differentialis* (Thos.) and *Melanoplus mexicanus mexicanus* (Sauss.) proved to be general feeders. Tests of *Brachystola magna* (Girard) show that this species is rather limited in its food choices. Only certain coarse weeds and cotton have been acceptable as food.

As far as migratory activities are concerned very little evidence was found of migration in search of food by any of the 37 non-migratory species studied. This non-migratory behavior is significant from the economic viewpoint. Field studies (1931-37) show that after the host-plants of certain acridian species wither and die in unfavorable plant habitats, the grasshoppers in these habitats also die and do not migrate to cultivated fields or other pastures where food conditions are favorable.

[20] For migratory, gregarious, and destructive acridians Uvarov (1928, p. vii) urges that the term locust should be used.

[21] In north central Texas *Melanoplus bivittatus* Say, is occasionally found and one would expect to find *Melanoplus femur-rubrum* (DeGeer). However, during the past seven years of field work (1931-37) only one specimen of *M. femur-rubrum* has been collected.

There is always a possibility however that species which find crop plants palatable (Tables 1-3) may to some extent, at least, be a threat as potential pest grasshoppers.

PHYSIOLOGY AND TAXONOMY

The menu differences of *Hesperotettix viridis viridis* (Thos.) and *Hesperotettix viridis pratensis* (Sc.) have been noted by Carothers (1923, p. 10). Field observations and cage studies of the writer show that these sub-species are definitely different in their distribution and in their food preferences. In north central Texas *H. v. viridis* is common and widely distributed. Its preferred food plant, Amphyachyris, is an abundant late summer and fall pasture weed. *H. v. pratensis,* however, is found in only a few localities. Its distribution is definitely restricted by the distribution of its favorite host-plant *Solidago petiolaris* Ait. These food selection differences appear to be correlated with the taxonomic differences of these grasshoppers. The question naturally arises are these physiological differences sufficient grounds to warrant the separation of *H. v. pratensis* from *H. v. viridis* and give the former specific rank.

The possibility of hybids among acridians is always of interest to taxonomists, as well as geneticists and cytologists. I have observed, as have others, a few instances of copulation in cages between *H. v. viridis* and *H. v. pratensis.* Similar pairing behavior was noted occasionally between other species. One unexpected instance was copulation between such widely separated species as *Hypochlora alba* (Dodge) and *Melanoplus plebejus* (Stål).

EXPOSURE OR SHELTER

Shelter afforded by vegetation undoubtedly plays an important role in acridian distribution. Certain species *Trimerotropis pistrinaria* Sauss., *Platylactista aztecus* (Sauss.), *Rehnita capito* (Stål) always live in open habitats on bare soils with only scattered clumps of vegetation, or even on eroded slopes with scant marginal vegetation; others, *Mesochloa abortiva* Bruner, *Opeia obscura* (Thos.), and *Trachyrahachis kiowa fuscifrons* (Stål) frequent low sparse vegetation, buffalo grass, Bermuda grass, clipped golf fairways; still others reach optimum numbers only among tall grasses and weeds, *Syrbula admirabilis* Uhler, *Hesperotettix viridis viridis* (Thos.), *Hesperotettix speciosus* (Sc.); a few frequent the open woods or timber margins, *Spharagemon bolli* Sc., *Chortophaga viridifasciata* (DeGeer), and *Psoloessa texana texana* (Sc.). The above are just a few examples of habitats showing variations in vegetation and cover, which are frequented by different kinds of grasshoppers.

It is obvious that the acridians living in open situations are exposed to all extremes and variations of weather; temperature, humidity, wind, and rain; or desiccation, freezing, sweltering, and drenching. Preliminary experiments suggest that species living in exposed situations will endure

higher ranges of temperature and aridity than the species from sheltered habitats or lush vegetation habitats. Hamilton (1936) points out that his experimental studies suggest that temperature and humidity optima differ not only for different species but for different stages in the life cycle of the same species.

GENERAL DISCUSSION AND CONCLUSIONS

The results of the writer's food-preference experiments and starvation tests clearly establish the fact that specific plants are required as food by many acridian species of north central Texas. Food tests in which an abundance and variety of fresh plant food selected from the host-plant menu of certain acridian species, when offered to other grasshopper species, proved in many instances to be wholly unpalatable even to the point of starvation. These experiments show that vigorous individuals of many species will starve in the presence of an abundance of vegetation if their host-plant species are not included in the foods offered.

It is evident from these data if specific grass feeders are included that over 75 per cent of the 40 species studied in the writer's cages were selective in their diet choices and were definitely oligophagous. Oviposition behavior further emphasizes the need of specific diet for individual maintenance and normal egg laying.

The experimental findings of these studies are in the main at variance with other investigators who have studied the relations of the Acrididae to plants or have reviewed literature on this subject. Uvarov (1928, p. 92) "Vegetation does not, however, influence the selection of habitat by many Acrididae as food because of its food value." Ross (1934, p. 128) "In many other groups of phytophagous insects the distribution of insect species is dependent primarily on distribution of the food plant. This is not true of the Orthoptera probably with few exceptions, such as *Inscudderia taxodii*, which is always found upon cyprus foliage." Vestal (1913, p. 77) "There is very seldom any direct relation between grasshopper species and species composition of the plant associations, as few grasshoppers are selective feeders." Golding (1934, p. 278) "The choice of habitat is not usually dependent on the vegetation *per se*."

The writer's experiments, on the other hand, point to the fact that many species of the Acrididae depend upon a limited number of plants for species maintenance. It is obvious, therefore, that plant species as food play an important role in distribution of many species of grasshoppers. However, other environmental factors are important in the make-up of a habitat complex when all different acridian species are considered. Among these other factors[22] soil texture, soil structure, topography, exposure, and vegetation as cover have been discussed. All of these must be evaluated in determin-

[22] Facilities were not at hand to determine soil moisture and pH. Soil moisture is, on the one hand related to soil texture, and on the other hand correlates with vegetation as cover for shade.

ing local distribution. Mere abundant growth of vegetation of the right plants for food is by no means the only criterion for acridian optimum living conditions. For example, a hillside slope covered with a pure stand of Evax has been examined and not a single specimen of *Acrolophitus variegatus* (Thos.) found although its host-plant (Evax) was everywhere abundant and *A. variegatus* was frequent in neighboring pastures where other conditions for its living were supplied. Eroded ridges with occasional plants of Hymenopappus are favored by *Trimerotropis pistrinaria* Sauss., rather than more level tracts with a solid cover of its favorite food plant, Hymenopappus. Other instances may be multiplied. The point at issue, however, is that specific plants, or at most a limited number of species, are among the *minimum conditions* necessary for species maintenance for many of the Acrididae. Specific plants as food cannot be left out of the picture and must be taken into account in explaining *local distribution of acridians.*

SOILS VS. VEGETATION

The writer's field evidence concerning soils chosen for oviposition by female grasshoppers of several species is more definite than are the results of his experimental studies obtained by testing the reaction of female acridians to different types of soil in cages. Table 7 gives suggestive data concerning the egg laying behavior of eighteen species. A few species, however, either did not react favorably to cage environments, were not supplied with the right kinds of foods, or their eggs were not matured. At least, very few egg pods were obtained although adult females were kept in cages for several weeks.

The types of soils, plants for food, vegetation for shelter and protection are among the environmental factors which suggest the grouping of the acridians studied into four classes: (1) The distribution of certain species seems clearly correlated with specific soil types. In certain cases (a) soil texture, such as sandy, sandy loam, clay loam, or clay (Weaver and Clements 1929, p. 168), appears to determine the soil choices, and in other cases (b) soil structure becomes the determining factor in the form of compact roadways, field margins or eroded hillsides. (2) Other species are limited in their local distribution by the presence of specific plant species for food. (3) Still other species depend on vegetation for shelter and protection. (4) There is a broadly tolerant class whose species appear to adjust themselves to variations in soil and vegetation.

In the main these affinities appear to follow taxonomic sub-family cleavages. (1) The Cyrtacanthacrinae are more definitely associated with specific plants for food. (2) The Acridinae are often dependent on plants for shelter and protection. The elongated body form of certain species simulates the shape of the upright culms of the tall prairie grasses; other Acridinae belonging chiefly to species of smaller size are somewhat flattened in body form, these are associated with low matted grasses. (3) The Oedipodinae are

the premier soil grasshoppers and are more obviously soil-related, not only in color and form, but even in oviposition behavior. Species of this sub-family, on the one hand, are clearly related to vegetation for shelter, shade and the resulting higher humidity [*Arphia simplex* Scud., *Chortophaga viridifasciata* (DeGeer)] or on the other hand there are species which are adapted to endure extremes of aridity and exposure where the vegetation is sparse [*Trimerotropis pistrinaria* Sauss., *Rehnita capito* (Stål)]. These variations in conditions have to be evaluated in explaining the distribution and soil relations of the Oedipodinae. (4) The Cyrtacanthacrinae and the Oedipodinae both contribute to a broadly tolerant or highly adaptive group. Certain species of these two sub-families are mixed feeders. These species frequent soils of varying texture although there is doubtless much uniformity in the matter of soil structure, as well as similarity in their shelter relations.

There are a number of clean-cut exceptions to the sub-family grouping I have suggested above. *Acrolophitus variegatus* (Thos.) is an interesting exception. In fact the collector who has studied the taxonomy of acridian sub-families would place this species with the Oedipodinae when first taken instead of the sub-family Acrididae. Even in its behavior *A. variegatus* lines up with the Oedipodinae. It frequents bare soils or rests on low, flat, broad-leaved plants. Another exception is found in *Psoloessa t. texana* (Sc.). This species and *A. variegatus* are more definitely soil related than any other species of the Acridinae of north central Texas. Several other exceptions might be given. In general, however, the affinities as outlined above will bear close field scrutiny.

SUMMARY

1. Many acridian species are selective feeders and are essentially oligophagous.

2. A few of the oligophagous grasshoppers approach monophagy.

3. Of the two chief north central Texas (1931-1937) economic species *Melanoplus differentialis* (Thos.) is strikingly polyphagous but *Brachystola magna* (Girard) is oligophagous.

4. Less than 25%, of the species experimentally tested in cages were mixed feeders and, appeared to even approach polyphagy.

5. The Acridinae and Oedipodinae were primarily grass eaters, selecting widely among the grasses offered in cages; however, under primitive conditions of the blackland prairies the number of species of grasses available was undoubtedly limited.

6. The Cyrtacanthacrinae fed chiefly on forbs. Selective feeders are more generally found in this sub-family than among the Acridinae, Oedipodinae, or Batrachotetriginae.

7. Starvation food experiments prove that selective feeders will starve in cages if deprived of their host-plants even in the presence of abundant fresh host-plant materials palatable to other species of the Acrididae.

8. A thorough understanding of acridian taxonomy with a knowledge of plant species is necessary before even a beginning can be made toward a comprehensive diagnostic analysis of local distribution of the Acrididae.

9. Soil factors which control the local distribution of plants are secondarily controlling factors of acridian distribution.

10. A few acridian species, especially among the grass eaters, appear to have identical menus, and in the field they show similar reactions to environmental conditions of exposure or shelter as the case may be. Their soil relations, however, are definitely different. For these species soil relations may be primary in determining their local distribution.

Soil structure appears to be more important in delimiting egg laying sites than soil texture; however, soil texture gives invaluable field clues in the marking off of terrestrial habitats.

11. The adaptation of certain acridians to introduced species of plants (Bermuda grass, Johnson grass, crop plants, et al.) has complicated the problem of local distribution.

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THE OYSTER "LEECH," *STYLOCHUS INIMICUS* PALOMBI, ASSOCIATED WITH OYSTERS ON THE COASTS OF FLORIDA

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THE OYSTER "LEECH," *STYLOCHUS INIMICUS* PALOMBI, ASSOCIATED WITH OYSTERS ON THE COASTS OF FLORIDA

INTRODUCTION

Among the pests which have decreased the productiveness of oyster beds on the Atlantic and Gulf coasts of the United States the polyclad worm which is known to Florida fishermen as the oyster "leech" has often attracted unfavorable attention. This flatworm has been reported to occur from Pensacola Bay on the west to Indian River on the east. At Tampa it has been known for more than thirty years, and according to Danglade (1919) it has become abundant enough to do considerable damage every few years. In 1906-1907 it destroyed oysters along the Indian River. In 1916-1917 it did much damage to beds at Cedar Key, Port Inglis, and Tampa. More recently the oyster leech has been abundant in Apalachicola Bay. Dr. H. F. Prytherch of the Beaufort Laboratory of the Bureau of Fisheries was sent to investigate conditions. In a typewritten report concerning his findings he says:

A few specimens of the wafer "leech" have been found by oystermen in Apalachicola Bay at various times in the past but not until 1932 had it become sufficiently abundant to seriously affect oyster production on natural bars. In November of that year the Bureau's investigation showed from 50 to 75 percent of the large oysters on Porter's Bar had been killed by the wafer and that approximately 25 percent of the live oysters contained one to four parasites each. During the following year all the oysters on this area were killed as well as a high percentage of those on adjacent natural beds known as Platform Bar, Green Point Bar, and North Lump. A recent survey of the above areas in October 1934 showed not only complete destruction of adult oysters but also a high and parasitic infection of the seed oysters which had attached here within the last year. It was evident that the parasite was spreading rapidly to other areas to the westward as it was found at several points on St. Vincent Bar, a distance of 12 miles from the original outbreak and on Bulkhead Bar, both of which are the largest natural oyster beds in this region.

The oyster industry in Apalachicola Bay began in 1836. Swift (1897) made a careful survey of the bay in 1895-1896 and published an excellent map. He states that,

The destruction of the beds in St. Vincent Sound and Apalachicola Bay was due somewhat to their being overworked, but principally to the following causes: The freshet of 1893, the hurricane of October 8, 1894, a very severe freeze in the latter part of December of the same year, and another very heavy hurricane on February 13 and 14, 1895. There had been previously (in January, 1886) a heavy freeze that killed many oysters, so that few were taken the following season, and in 1888 a freshet seriously affected the beds.

It seems to be the general opinion that the beds are deteriorating at Platform, Bulkhead, and Cat Point bars, where oystering is going on at present, and the reason assigned is that beds are overworked, the demand being too great for the supply. As far as known there seem to be no enemies of the oysters on the beds, unless the boring clam . . . and the algae found on the oysters of the East Hole Bar may be called enemies.

Again in 1915 Danglade (1917) surveyed and mapped Apalachicola Bay. He says "the oysters of these waters have no aggressive enemies, and no diseases were observed. Physical phenomena, however, have greatly damaged many of the bars." Soon after this, early in 1917, oyster leeches were reported as doing damage to beds at several points on the east coast of Florida and Danglade (1919) made an investigation. He found that leeches were most abundant on bars where salinity was high. "When the devastation was at its height the affected oysters, as a rule, contained from 1 to 3 worms, although as many as 8 or 10 are said to have been taken from a single oyster . . . in Tampa Bay . . . mature and young oysters alike were said to have been completely annihilated. . . . At Port Inglis and Cedar Key . . . no small oysters were found or reported containing worms."

The writers of the present paper were asked to go to Florida to study the oyster leech for the Bureau; and spent eleven months beginning June 1, 1935 in Apalachicola Bay, with short trips to other parts of the state. Two species of oysters, *Ostrea virginica* Gmelin and *O. equestris* Say, were found on the bars in Apalachicola Bay. With these, two species of polyclad worms were regularly associated and eight other species of polyclads were present at times. The work was carried on at the Indian Pass Laboratory of the Bureau. It is a pleasure to make the following acknowledgments: Mr. Elmer Higgins offered the opportunity to carry on the work and did everything possible to make it a success; Dr. Paul S. Galtsoff gave encouragement and valuable advice; Dr. H. F. Prytherch turned over all records of his work on polyclads in Florida and made many helpful suggestions; Mr. George S. Hiles, Jr. determined routine salinities for the laboratory until March 1; Captain Frederick Sawyer and Herbert D. Lane, crew of the boat *Virginia,* gave most excellent, cheerful, and competent service in collecting and helping in the examination of materials from the oyster bars; and Mr. R. O. Smith helped in administrative matters. A number of specialists identified certain of the animals collected and grateful acknowledgment is made for their services: algae, Dr. H. L. Blomquist; coelenterates, Dr. Oskar Carlgren; polychaetes, Dr. A. H. Treadwell; echinoderms, Dr. C. B. Wilson; amphipods, Mr. C. R. Shoemaker; isopods, Mr. J. O. Maloney; anomurans and macrurans, Dr. Waldo Schmitt; crabs, Dr. Mary J. Rathbun; bugs, Dr. H. B. Hungerford; insect larvae, Dr. J. G. Needham; molluscs, Dr. Paul Bartsch and Harold Rehder; ascidians, Dr. W. G. Van Name; fishes, Dr. S. F. Hildebrand.

ANATOMY

Stylochus inimicus Palombi 1931 is classified as follows: Platyhelmintha, Class Turbellarea, Order Polycladida, Suborder Acotylina, Section Craspedommatina, Family Stylochidae, Subfamily Stylochinae; hence is characterized by a flat, leaf-like, firm, parenchymatous body; ciliated integument; ventral mouth, plicated pharynx, and many-branched enteron; brain surrounded by a parenchymatous capsule; reticulate nervous system with several chief longitudinal trunks; nuchal tentacles, but none on margin; marginal, tentacular, cerebral, and frontal eyes; no statocysts; hermaphroditic genital system; male genital apparatus anterior to female and both near the posterior end; reproduction only by sexual means; development results in a ciliated pelagic larva; adult is free-living or commensal.

GENERAL FORM AND SIZE—The body is flat, elliptical and often has the margins wrinkled slightly. The largest specimen from Apalachicola Bay when alive and extended measured 51 mm. long and 27 mm. wide while crawling actively; resting, 40 by 31 mm. It was collected on Porter's Bar, November 7, 1935. The whole surface of the body is covered with close-set cilia, which range from 0.001 to 0.005 mm. in length.

COLOR—The dorsal side is generally gray, with lighter margins and a light band along the middle of the median line. The ventral surface is gray to dirty-white at the margins and grows lighter toward the center, where there is a large white spot caused by the pharynx and parts of the reproductive organs showing through the integument.

ENTERON—The mouth is a small opening (Fig. 1, m) nearly in the center of the ventral surface. It opens into a pouch which contains the pharynx and this leads into the median stem of the gastro-vascular system. The elongated pharynx has about six pairs of folds along its sides. These may be extended through the mouth when food is being swallowed (Figs. 2, 3, 4). From the median enteric stem branched caeca extend almost to the margins of the body: 1 anterior, 1 posterior, and about 8 pairs lateral.

NERVOUS SYSTEM AND SENSE ORGANS—At about the posterior margin of the anterior fifth of the body are two slightly tapering, conical dorsal tentacles. In a moving individual these are about 0.5 mm. long and 2.0 mm. apart. They are usually symmetrically disposed on either side of the body but in some individuals one tentacle may be more or less anterior to the other. The tentacles are retractile and may be withdrawn completely into non-pigmented depressions in the dorsal surface. Between the tentacles is a ganglionic mass. From this four nerves extend forward, three laterally, and a slender dorsal and a heavy ventral pair posteriorly. There are many connections between the principal nerves so that the whole system forms a nerve net (Fig. 5). Along the margins there are also many fine connections between the smaller nerve twigs, and thus a delicate reticulum is built up. A typical adult leech possesses perhaps 1,600 black eye spots. Those in the

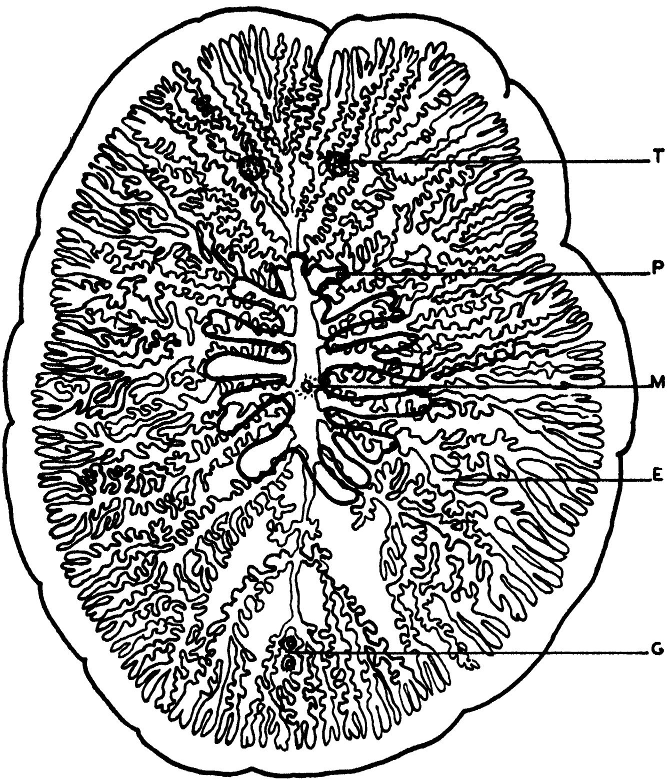
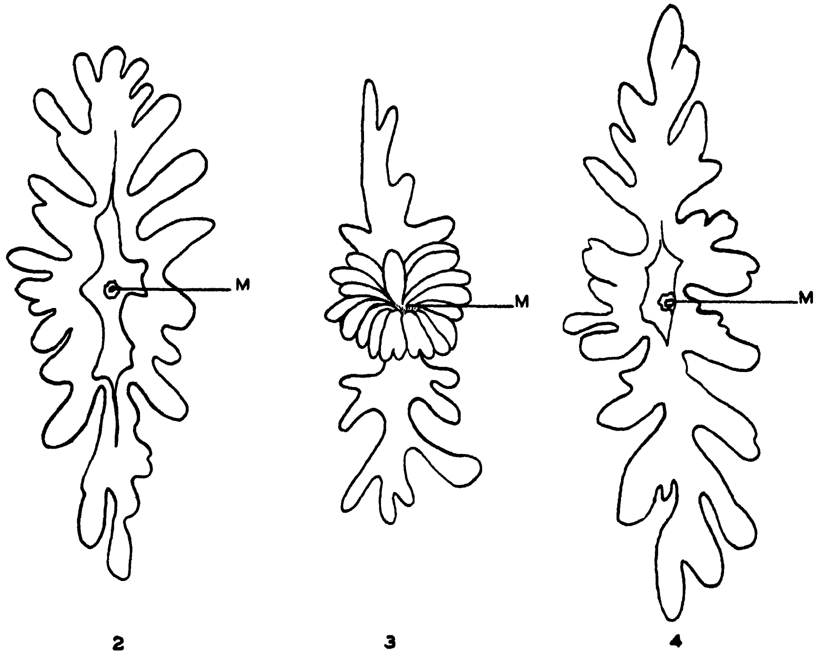


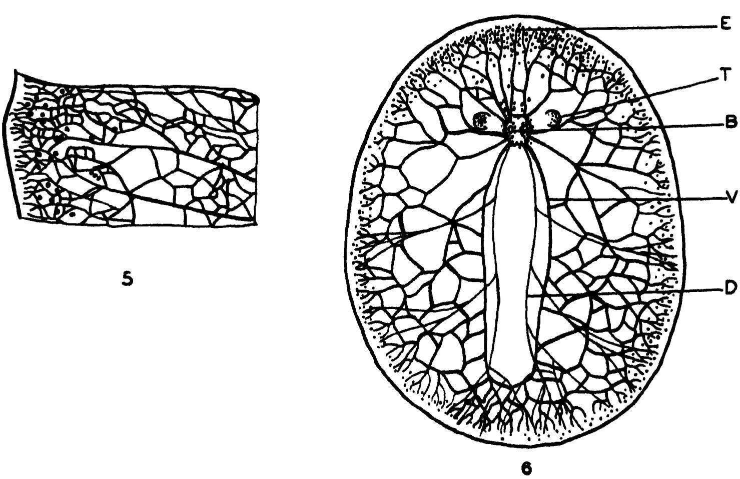
Fig. 1. Enteron of *Stylochus inimicus*. *E*, lateral branch of enteron; *G*, genital openings; *M*, mouth; *P*, pharynx; *T*, nuchal tentacles.

tentacles are largest; those at the anterior margin are rather large and there is a general decrease in size and number toward the posterior end, but there are fewest along the postero-lateral margins. The eye spots in an adult leech are distributed as follows: proximal four-fifths of tentacles, 80; two irregular rows of spots dorsal and anterior to the cerebral ganglia, 160; anterior quarter of margin, 720; anterior half of margin, 920; posterior half of margin, 440; posterior quarter of margin, 220.

Genitalia (Fig. 7)—The male genital opening is in the median line one-seventh of the length of the body from the posterior end. It is surrounded by an oval muscular area. This is doubtless concerned with the protrusion of the penis which lies immediately inside of and anterior to the opening. The duct from the fuzzy prostate gland and that from the seminal vesicle join anterior to the penis to form the short ejaculatory duct. The prostate gland is just dorsal and anterior to the penis. The seminal vesicle is ventral and slightly anterior to the prostate gland. From the seminal vesicle two twisted vasa deferentia lead antero-laterally and may be traced respec-



FIGS. 2-4. Pharynx in various stages; in 3 it is being extended through the mouth, *M*.



FIGS. 5-6. Nervous system. 5, detail to show distribution of nerve twigs and eyes along left anterior margin. 6, plan for whole body; *B*, brain; *D*, dorsal nerve trunk; *E*, marginal eyes; *T*, nuchal tentacle; *V*, ventral nerve trunk.

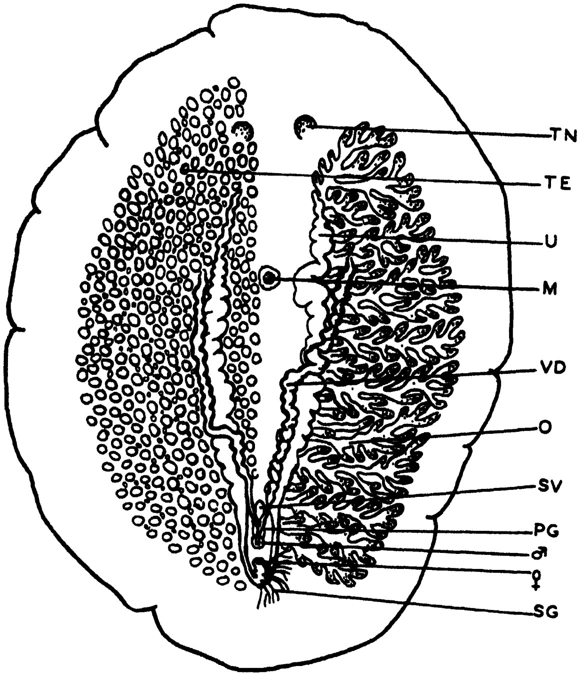
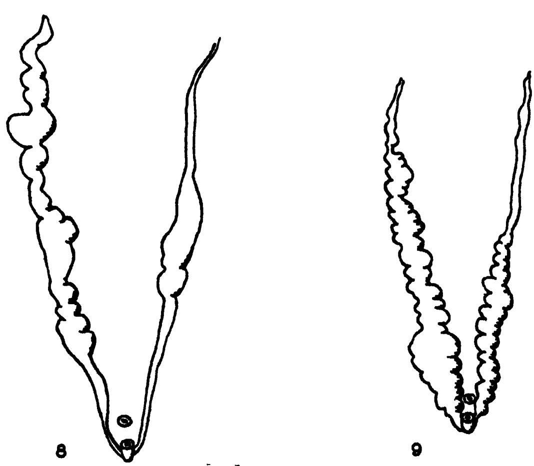


FIG. 7. Genital system: *M*, mouth; *O*, ovarian follicles; *PG*, prostate gland; *SG*, shell gland; *SV*, seminal vesicle; *TE*, testes; *TN*, tentacles; *U*, uterus; *VD*, vas deferens; ♂ male; ♀ female.



FIGS. 8-9. Two pairs of uteri distended with eggs.

tively to points about halfway between the mouth and the lateral margins. On each side about 350 testes of various sizes are scattered through most of the available space. The longest of the testes measure about 0.02 mm. The female genital opening is about 0.2 mm. behind that of the male. It leads into a short (0.2 mm.) vagina. This in turn is connected with two lateral curved uteri which extend forward latero-dorsal to the vasa deferentia and end lateral to and about 0.3 mm. behind the tentacles. From the uteri oviducts and ovarian tubules extend laterally to within 0.2-0.5 mm. of the margin. The tubules are branched somewhat and end in blunt tips.

SECTIONS—Transverse and sagittal sections of individuals were mounted and stained with hematoxylin and eosin. They show no essential differences from the descriptions and figures published by Palombi (1931, 1936). It therefore seems unnecessary to discuss them.

LIFE HISTORY

BREEDING—The eggs of Stylochus are fertilized internally by spiral spermatozoa (Fig. 11) about 0.04 mm. in length. Fertilized ova are stored in the paired uteri. In the field eggs were found adhering to the clean inner surfaces of old shells on the oyster bars from the beginning of our observations (June 1) until January 11, but the last eggs failed to develop when brought into the laboratory and may have been laid sometime previously and killed by low temperatures. Throughout the summer when several individuals were placed together in a dish in the laboratory they were seen crawling backwards with the posterior end elevated and the penis extended. Copulation was carried on for as long as nine hours. One pair copulated for five hours on one day, separated, and began again the next day. Several individuals copulated more than once; some at least four times.

OVIPOSITION AND FECUNDITY—Stylochus readily deposits eggs on hard surfaces and then broods them for days. Inside old shells on oyster bars

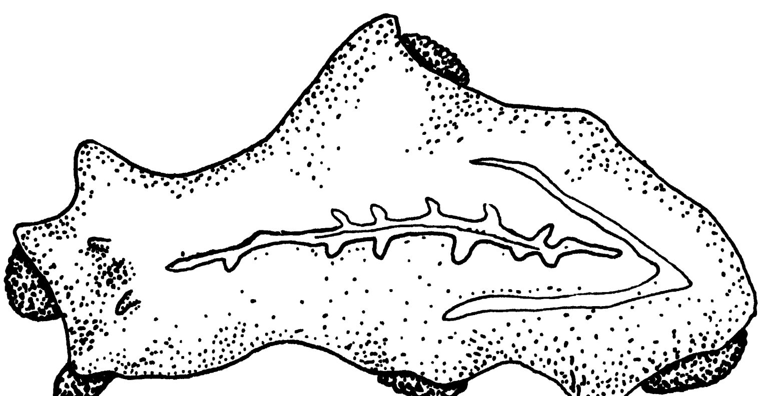


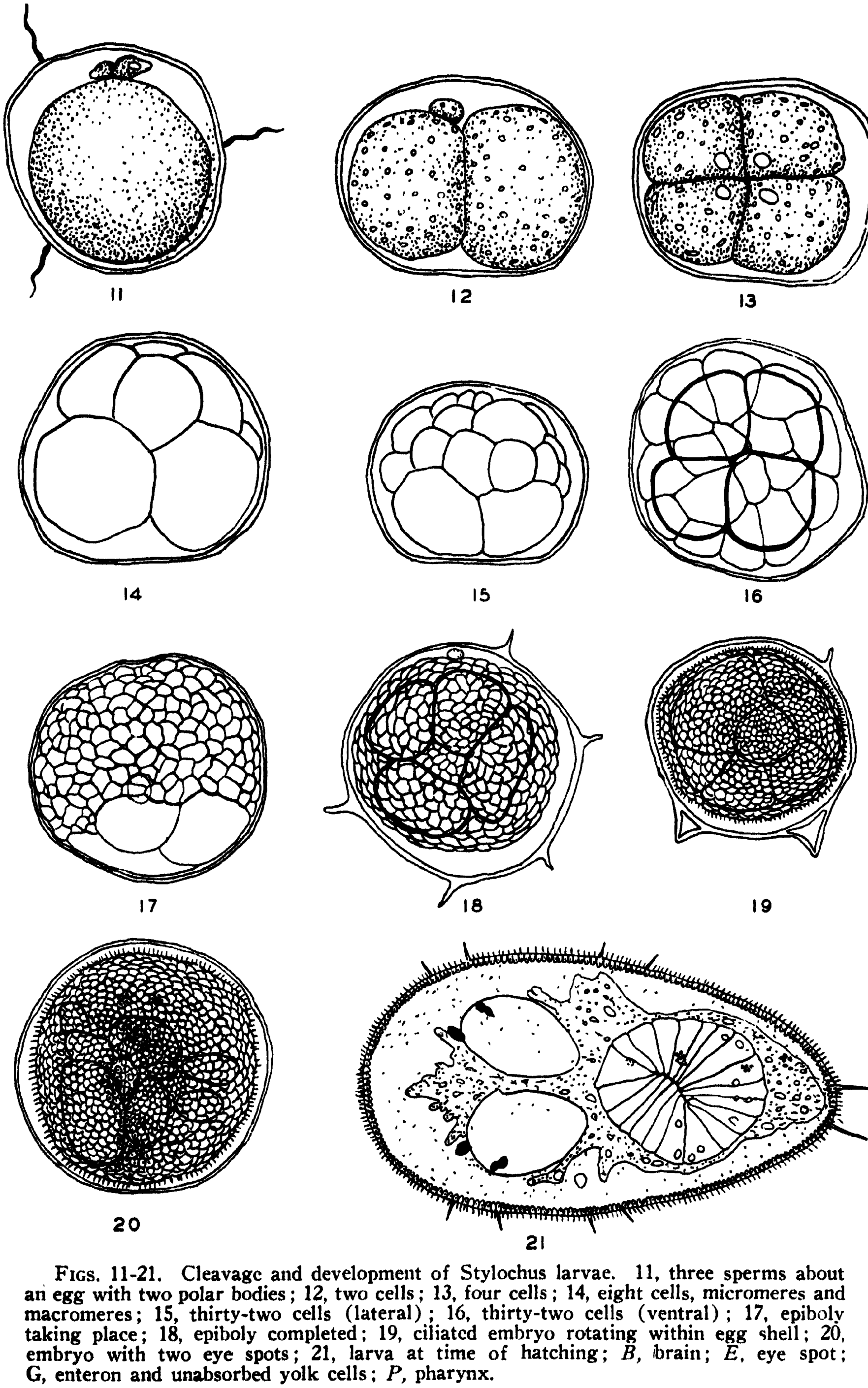
FIG. 10. Shape assumed by a Stylochus brooding a large group of eggs that had been laid by several individuals.

and in finger bowls in the laboratory many clutches were observed. Eggs are laid in irregular masses which are a single layer thick. Each egg is enclosed in a shell (Fig. 11), the diameter of which is about 0.18 mm. When fresh-laid the shell is sticky and adheres to the surface below it and to other shells in its group. The brooding instinct is very strong. In September some Stylochi were kept together in a dish and several contributed to a large, irregular mass of eggs. One large individual then spread itself into a very bizarre shape (Fig. 10) in order to cover the mass and so remained from September 3 to 11—eight days. In the field single Stylochi were often found brooding clutches of eggs which all appeared to have been laid by one individual. Six clutches were carefully counted under a binocular microscope and were found to number: 18028; 17267; 15025; 14252; 11275, and 9158. In the laboratory 35 individuals with full uteri were selected for observation and 31 clutches of eggs were obtained. Six individuals which were kept separately in finger bowls without food laid eggs as follows:

No. 1—July 30, 15072; August 14, 5979; August 21, 919; total, 21970.
No. 2—July 30, 14022; August 15, 1970; total, 15992.
No. 3—July 29, 10179; August 7, 3190; total 13369.
No. 4—July 29, 7351; August 15, 1509; August 21, 2447; total, 11307.
No. 5—July 27, 9075.
No. 6—July 27, 7818.

Of course any or all of these worms may have laid eggs before they were brought into the laboratory. Most of the eggs seemed to be fertile and developing normally. Eggs were not always in the 1-cell stage when laid. For example, six clutches when deposited in the laboratory on July 4, 1935, were in the following cell stages: 1-cell stage, 1 to 2-cell stage, 1 to 8-cell stage, 4 to 16-cell stage, 4 to 16-cell stage, and 8 to 32-cell stage.

EMBRYOLOGY (Figs. 11-21)—Eggs in different clutches appeared to develop at about the same rate (depending on temperature, salinity of medium, etc.), but there were often variations in the time which elapsed between stages. During cleavage the following intervals were observed in times required to pass from one stage to the next at 28.0°C. 1-2 cells, 1 h. 9 m., 2 h. 17 m.; 2-4 cells, 2 h. 41 m.; 4-8 cells, 4 h. 10 m., 34 m.; 8-12 cells, 3 m., 10 m., 3 m.; 12-16 cells, 5 m., 7 m., 3 m., 27 m.; 16-32 cells, 1 h. 45 m., 2 h. 36 m., 2 h. 26 m. At room temperatures (28°C. ±) in the laboratory eggs required about 11 days to hatch. Progress was about as follows each day: (1) 64 cells, (2) epiboly partly completed, (3) ciliated epidermis and embryo rotating slowly within the egg shell, (4, 5, 6) cilia visible on outside and embryo rotating more rapidly, (7) two eyes present, (8) four eyes present, (9) four eye spots persisted, two posterior setae and a ventral mouth appeared, (10) six eyes present, (11) ciliated, 6-eyed larva hatched.



FIGS. 11-21. Cleavage and development of Stylochus larvae. 11, three sperms about an egg with two polar bodies; 12, two cells; 13, four cells; 14, eight cells, micromeres and macromeres; 15, thirty-two cells (lateral); 16, thirty-two cells (ventral); 17, epiboly taking place; 18, epiboly completed; 19, ciliated embryo rotating within egg shell; 20, embryo with two eye spots; 21, larva at time of hatching; *B*, brain; *E*, eye spot; G, enteron and unabsorbed yolk cells; *P*, pharynx.

When eggs were deposited a polar body was usually apparent at the animal pole. It often divided into two or more cells; and sometimes appeared to multiply into a mass of many cells. It often persisted as an appendage to the developing embryo or as a free body within the shell. In 2- and 4-cell stages blastomeres were nearly equal in size, but in the 8-cell stage four micromeres and four macromeres were formed. The micromeres divided more rapidly, and during the second day began to overgrow the larger, yolk-laden macromeres (called micromeres by MacBride 1914). After the macromeres were invested by ectoderm they retained their identity for a day or two but soon broke up into irregular masses which gradually accumulated considerable pigment. Eyes were first present on the seventh day. They apparently increased in number by division of the first pair formed. When first deposited shells were creamy white as seen with the naked eye, but when ready to hatch were covered with a brown coating.

Pelagic Larva—After hatching, the ciliated, setose larva (Fig. 21) soon began to swim about. It took an erratic course, continually whirling about, but groups of larvae congregated near the surface of dishes where light was most intense. Many were caught above the surface film and died on the sides of dishes. Larvae swam at the rate of about 1.32 mm. per second at 25°C. One larva swam upward 115 cm. through a glass tube (which had a bore 12 mm. in diameter) in 12 minutes and 30 seconds. Larvae appeared to be strongly positively phototropic, slightly negatively rheotropic, and rather unresponsive to gravity and temperature variations.

Growth—On February 7, 1936 ten *Eustylochus meridianalis* were placed in separate finger bowls in sea water that had a salinity of 15.8 0/00. They were given oyster and fresh sea water (15.8 0/00) on alternate days. Two died on February 18 without growth; another on February 24; five others on March 5. The remaining worm ate oyster and increased in length as follows: February 8, 1.5 mm.; February 18, 2.5 mm.; February 24, 3.5 mm.; March 5, 4.5 mm.; March 22, 10 mm.; March 31, 10 mm.; April 2, 12 mm. On the last date it was sexually mature, and apparently in good condition. The same individual was taken to Beaufort, N. C. It was fed oyster until May 16, and had then attained a length of 20 mm. It grew to maturity in less than two months. This Eustylochus was fixed, imbedded, sectioned, and stained. Spermatozoa and ova were found to be abundant in its vasa deferentia and uteri. It had never been with another individual, and had therefore not copulated.

On March 5 two lots of five each of Eustylochus were fed on alternate days; one with oyster and the other with barnacle. The results of this work are summarized in Table 1. These results show that the growth of Eustylochus may be quite rapid under favorable conditions.

Stylochus also grows rapidly. At Oslo and St. Lucie, Florida, seventy-seven Stylochi were collected on April 7 and 8, but none were taken when

TABLE 1. GROWTH OF *Eustylochus meridianalis* FED ON OYSTER OR BARNACLE

Date	5 specimens fed oyster				5 specimens fed barnacles			
	Eyes		Length		Eyes		Length	
	Average Number	Per cent Increase	Average mm.	Per cent Increase	Average Number	Per cent Increase	Average mm.	Per cent Increase
March 5 .	12	0	1.6	0	13.8	0	1.4	0
March 14	20	40	1.9	19	23.8	101	2.6	100
March 22 .	Dead[1]		Dead[1]		75.0	543	5.2	207

[1]These were apparently killed by the fouling of water by spoiled oyster.

buckets of shells collected from oyster bars were allowed to stand overnight. All but five of these specimens were of large size and thirty-four of them were brooding clutches of eggs. The larger individuals had probably passed the winter in a rather mature condition and began to breed early in the spring. The largest individuals measured 25 to 48 mm. in length; the five small individuals, 10-20 mm., ave. 14.6 mm. The latter were fed oyster from April 9 to 20 at the Indian Pass Laboratory and then shipped to Beaufort, N. C. where they were fed oyster daily until May 20. At the beginning of the experiment at Beaufort their average length was 12 mm. and their average weight 0.0366 grams. During three weeks their length increased 43% and their weight 112%, i.e.; to 17.2 mm. and 0.775 grams. Probably most Stylochi live less than one year.

STARVATION—Five specimens of *Stylochus inimicus* were kept in separate covered finger bowls in the laboratory from November 18 to March 5, without changing the water in the dishes or feeding the worms. After March 5 two of the worms were placed together in a dish. These individuals were fed oyster every other day and fresh sea water was used in their bowl. The other three worms were kept as before. The two fed worms apparently ate nothing, but became active and copulated. On November 18 the length of the worms was respectively: 30, 25, 23, 23, and 20 mm.; on March 5 it was 12, 22, 20, 18, and 11 mm. All had decreased in size. The third and the fifth in the list laid eggs on or before November 29. One of these starved Stylochi lived until May 21 at Beaufort, N. C., a total of 185 days without food.

PHYSIOLOGY

LOCOMOTION—Below 12°C. and above 34°C. Stylochus usually curled up and did not attach itself to the substratum. The righting reaction appeared to give a better index of the activity at different temperatures than actual rate of locomotion, as the curve in Figure 22 shows. On a smooth glass or celluloid surface, tested in sea water having a salinity of about 20 0/00 Stylochus crawled at the following rates in millimeters per minute:

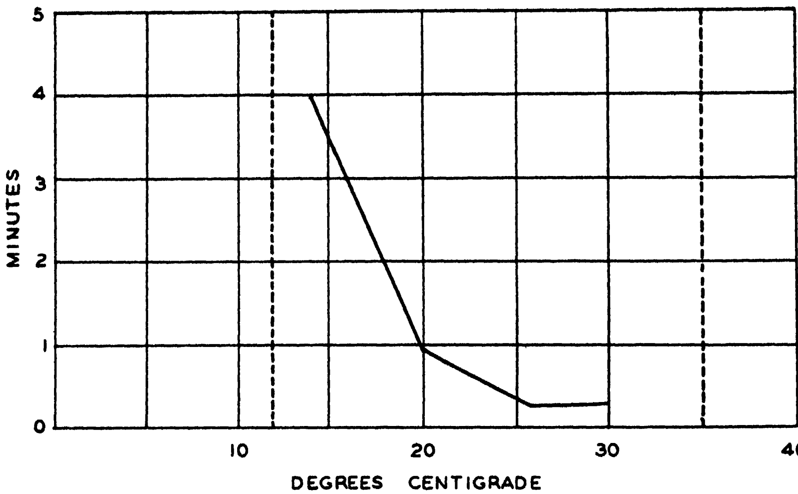


Fig. 22. Average time, in relation to temperature, taken by Stylochus which had been turned with its ventrum uppermost to right itself and become attached to the substratum. The vertical dotted lines indicate the thermal limits of attachment.

14°C., 6.6; 14.9°C., 15.6; 19.7°C., 26.4; 23°C., 35.4; and 25°C., 39.2. Of course large individuals usually moved faster than small, and there was considerable individual variation. Stylochus crawls on the edges of its body so that there is a cavity below. It continually jerks its anterior margin, now in one region and again in another, as it moves forward. The tentacles are turned forward a little. Often an individual may crawl backward for a short distance. A Stylochus is readily fatigued. One individual moved 85 cm. at an average speed of 35.4 mm. per minute. At the beginning it moved 52.8 mm. per minute, at the end, 27.6 mm. *Eustylochus meridianalis* is active at lower temperatures and in general moves more rapidly than Stylochus; as the following rates in millimeters per minute show: 7°C., 0.12; 12°C., 19.8; 14°C., 26.4; 15°C., 24.0.

Permeability—At the suggestion of Dr. Paul M. Gross preliminary experiments on the behavior of eggs in a graded series of salinities were performed in the hope that they might throw some light on the permeability of egg shells. On December 3 eggs of Stylochus were collected from Crooked

Table 2. Effect of Immersing *Stylochus inimicus* "Eggs" for Thirty Minutes in Hypo- and Hyper-tonic Solutions of Sea Water; at 13.6 C. *a*, Alive; *ar*, Alive and Rotating; *d*, Dead

Salinity gms. per l.	0	5	10	15	20	25	30	35	40	45	50	55	75	90
Diameter, mm.	.181	.181	.180	.173	.158	.149	.147	.148	.159	.154	.172	.171	.176	.178
Condition	*d*	*d*	*d*	*a*	*ar*	*ar*	*ar*	*ar*	*ar*	*ar*	*ar*	*ar*	*ar*	*ar*

TABLE 3. EFFECTS OF IMMERSING *Stylochus inimicus* EGGS FOR ONE HOUR IN HYPO- AND HYPER-TONIC SOLUTIONS OF NaCl, AFTER BEING KEPT IN SEA WATER OF SALINITY 25 ⁰/₀₀ WHERE EGGS HAD AN AVERAGE DIAMETER OF 0.140 MM. *a.* SOME ALIVE; *d.* DEAD; *dd,* DEAD AND DISINTEGRATING; *f.* FLOATING

Salinity gms. per l.	0	5	10	15	20	25	30	35	40	45	50
Diameter mm.	.188	.207	.163	.152	.153	.142	.139	.146	.155	.160	.162
Condition.	*dd*	*d*	*d*	*a*	*d*	*d*	*d*	*df*	*df*	*df*	*ddf*

Island Sound where salinity was 33.4 0/00. These were in about the fourth day of development (Fig. 19), with ciliated eyeless embryos within the egg shells. The average diameter of an egg in a sample of ten from the general stock was 0.141 mm. The specific gravity of the eggs was 1.02 ±. Experiments were conducted at room temperature (13.6°C.) in the laboratory. Measurements were made after eggs had been in a solution for thirty minutes; an average of ten being taken in each case. The results are shown in Table 2 and Figure 23.

Experiments were also tried in which eggs of about the same age were immersed in various solutions of sodium chloride. The results are given in Table 3 and Figure 23. Evidently the increase in diameter of eggs is due to the movement of water through the egg shell to balance unequal osmotic pressure, which results from the change in the external medium. In dilute solutions the relatively high concentrations of salt within the egg shell compared to the low concentration without was responsible for the inequality in pressure. In the concentrated solutions the activity coefficients of the dissolved salts were less than those within the egg shell and so even though the concentration was higher the water moved into the egg instead of from it. The behavior of larvae and adults in various solutions will be discussed later under salinity and chemicals.

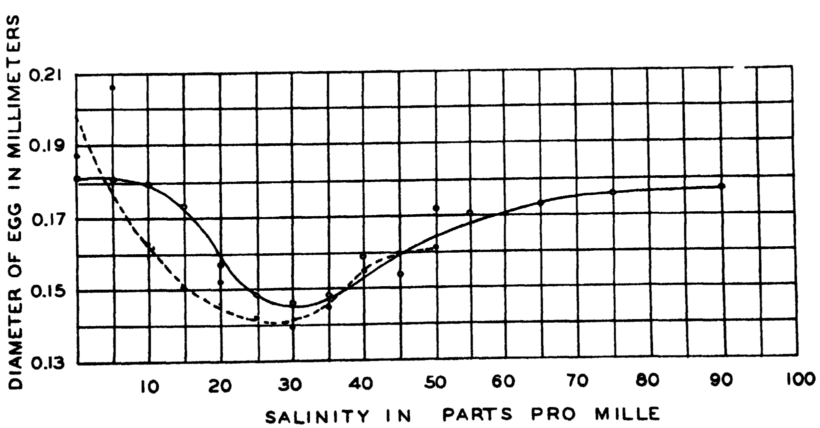


FIG. 23. Graphs showing size of eggs after being immersed for half an hour in sea water (- - - - -) or in a sodium chloride (———) solution.

OXYGEN RELATIONS—Two methods were used in testing the rate of oxygen consumption of Stylochi. Some worms were tested in a Warburg apparatus. Others were kept separately in closed citrate bottles which had been filled with clean sea water and completely immersed. In containers in which water was kept without worms as a control measure there was no decrease in oxygen. The bottles used had a capacity of about 390 cc. Every 24 hours a bottle was removed and the oxygen content of the water was determined by the Winkler method. In sea water in the Warburg apparatus at 26.5°C. and in a salinity of 10 0/00 a Stylochus used 0.100 cc. of oxygen per gram of body weight per hour; at 26.5°C., S. 30, 0.108 cc. In citrate bottles at 26° ± C. and a salinity of 20 0/00 Stylochi consumed about 0.098 cc. per body gram per hour. Large individuals used oxygen more slowly than small. When the worms were left in closed citrate bottles they used progressively less oxygen after the second day, but never exhausted all the oxygen present while alive. When an individual died and decayed there was no oxygen present. Table 4 gives the amount of oxygen remaining after several days in citrate bottles in which Stylochi had been kept, and Figure 24 shows the computed rate of oxygen consumption in the bottles.

TABLE 4. AMOUNT OF OXYGEN REMAINING AFTER ONE EXPERIMENT IN WHICH TEN *Stylochus inimicus* HAD BEEN CONFINED IN CLOSED CITRATE BOTTLES FOR SEVERAL DAYS. THE WORMS RANGED IN VOLUME FROM 0.09 CC. TO 0.31 CC.

Days	1	4	6	7	8	9	10
O_2, cc. per l..	5.5	0.076	0.09	0.14	0.12	0.10	0.15
	.		0.13	.	0.13	0.12	0.16

DESICCATION—Adult Stylochi are able to endure considerable desiccation; the eggs and larvae, very little. Fifteen individuals were wiped on clean cheese cloth, weighed, and allowed to stand in open glass dishes for air drying, and again weighed. Eleven which lost from 18.2 to 54.6 percent of body weight lived when placed in sea water; four which lost from 57 to 66.7 percent died. When twenty Stylochi exposed separately in air in uncovered clean finger bowls in the laboratory where humidity was 72 to 77 percent and temperatures were 25.2 to 25.5°C. one individual lived eight hours. When twenty were exposed in clean dry, covered bowls at temperatures of 25.3 to 26.5°C. one individual revived when placed in sea water after an exposure of fifteen hours in air. Its margin sloughed off, but the worm regenerated its body and became practically normal without food in about a month. Another individual moved feebly after an exposure of twenty-four hours in air, but died in a couple of days after being placed in water. In air of 66 percent humidity at a temperature of 27.4°C. all Stylochus eggs survived an exposure of 35 minutes in open, dry finger bowls; only 2 out of 1,000 lived 40 to 85 minutes. Some experiments were tried in

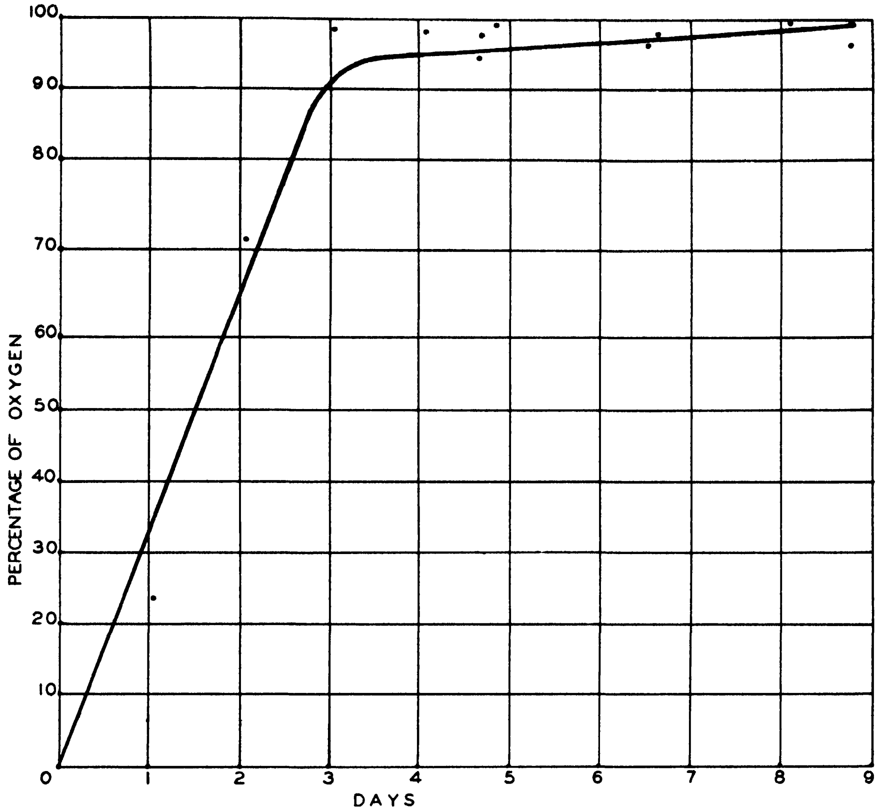


FIG. 24. Percentage of available oxygen consumed by Stylochi when left separately in sea water in closed citrate bottles. Volume of worms used ranged from 0.18 cc. to 0.31 cc.

which shell refuse was tonged up from oyster bars (Hagen's Flats; November 12, 3 P.M.), allowed to drain for a few minutes on the deck of a boat, and then placed in clean dry pails, which were placed outdoors where they were well protected from sun and wind. Water was added at twelve hour intervals to various pails; temperatures ranged between 12.5 and 20.4°C. Two living Stylochi were obtained from a pail in which shell refuse had been left without water for seventy-two hours. A similar test was made with pails tonged from East Hole on November 7; at temperatures of 17.4 to 23.6°C. living Stylochi were obtained when water was added to pails after forty-eight hours.

WATER CONTENT AND ASH—A Stylochus weighed about 0.222 grams per cubic centimeter. The ash from two lots of ten incinerated in an electric furnace was 2.1 and 2.4 percent of net weight (i.e.—weight after being wiped on cheese cloth). The percentage of dry weight after 18 hours in an oven at 36°C. was 23.8.

SALINITY—The general distribution of Stylochus on the oyster bars in Apalachicola Bay indicated that it flourishes best in rather high salinities. Observations in the laboratory support this view. Experiments were carried out in which Stylochi were transferred directly from sea water (S., 31.73 0/00) to various dilutions in finger bowls. Two worms were placed in each bowl and twelve were tested in each salinity. Under such conditions all of the worms died at salinities of 8 and 5 0/00 and most of them died at 11 0/00. However, when Stylochi were placed in pairs in finger bowls and transferred each day to gradually decreasing salinities some survived in dilutions of 6.42, 6.36, 6.07, and 5.88 0/00. Below 6 0/00 they curled and often failed to adhere to the substratum. Though Stylochi survived in rather low dilutions of sea water they usually did not lay eggs below salinities equal to about 15 grams per liter. Table 5 shows the number of eggs laid by Stylochi in various salinities. The number increases progressively from less to more salty dilutions of sea water.

TABLE 5. EGGS LAID BY EIGHTY *Stylochus inimicus* DURING TEN DAYS IN SEA WATER AND IN VARIOUS DILUTIONS; EACH WORM IN SEPARATE FINGER BOWL; 23.1 C. TO 31.5 C.; JULY TO AUGUST 10

Salinity	Number laying eggs	Average number eggs	Condition
4.90	0	0	Dead
8.19	0	0	Dead
11.31	0	0	Mostly dead
14.45	1	20[2]	Alive
17.76	6	403	Normal
20.95	8	1520	Normal
27.39	8	2112	Normal
33.87	7	2497	Normal

[2]Non-adherent and did not develop.

Stylochus larvae lived indefinitely when transferred directly from water having a salinity of 31-33.4 to 15.5 0/00; lived 45 minutes in 3.9; 10 minutes in 12.2; 7 minutes in 9.8; 3 minutes in 6.8; died at once and became opaque in 4.9 and 0.1 0/00.

Eustylochus meridianalis can tolerate lower salinities than *Stylochus inimicus.* In a pail of oyster shells and sea water collected from the north end of St. Vincent Bar February 17, and East Bay April 15 Eustylochi came to the surface and crawled about in salinities of 9.6 0/00; others were collected from pails in which salinities were 4.6, 3.2, 2.7, and 0.6 0/00. During January, when kept in finger bowls and subjected to gradually decreasing salinities four out of eight individuals lived in S. 2.93 0/00 for eight hours. When transferred directly from sea water (S. 32.2) to dilutions some lived in S. 6.44 0/00, but all died in S. 3.22 0/00. The swimming larvae of Eustylochus, when about 100 were transferred to dilutions, showed the following results after ten minutes: S. 30 to 15, normal; S. 10, about half dead; S. 9, several alive; S. 8, 7, few alive; S. 6, 5, 0, all dead.

Mr. C. F. von Herrman, United States Weather Bureau, has kindly furnished data for rainfall in Georgia and for the height of the Apalachicola River at Blountstown. His report (Climatological Data, Georgia Section 35:51) says "the year 1931 was thus the driest on the records for the past 40 years." This was followed by a great epidemic of oyster "leeches" in Apalachicola Bay during the following year (1932). Dr. H. F. Prytherch has constructed a graph which shows mean monthly river heights at Blountstown, Florida, from 1931 to 1934. His observations show that there have been more Stylochi in Apalachicola Bay during periods of drought.

CHEMICALS—In the hope that some chemical might be found which would be of value for killing oyster "leeches" twenty-five substances were tested in sea water during August, September, and October. The following list gives the lowest concentration which killed adult Stylochi:

0.001 percent—Beta naphthylamine.

0.01 percent—Potassium cyanide, sulfuric acid, shirlan N. A., Dupont shirlan D., para cresol, sodium hypochlorate.

0.1 percent—Sodium hydrate, potassium hydrate, hydrochloric acid, nitric acid, acetic acid, phenol, ortho nitro phenol, furfural.

1.0 percent—Ethylene chloride.

Saturated—Nitro benzene, brom benzene, naphthionic acid 1-4, Dupont shirlan crude, beta naphthylamine.

A 1.0 percent solution of sodium fluoride and a saturated solution of naphthelene had no apparent effect. Experiments with Stylochus larvae gave the following lowest concentrations which caused death:

0.001 percent—Copper sulfate, sodium hypochlorate.

0.01 percent—Potassium hydroxide, sodium hydroxide, beta naphthylamine, para cresol, shirlan, shirlan D.

0.1 percent—Hydrochloric acid, sodium fluoride, furfural, ethylene chloride, brom benzene, ortho nitro phenol.

Saturated solution—Nitro benzene (10%), naphthionic acid 1-4. In solution of some of the substances tested adult worms died variously. Sometimes a very strong solution caused the body to curl up tightly and stiffen without the secretion of mucus; whereas a weaker solution caused strong contraction, so that internal parts were squirted out through the integument, crinkling of margins, and abundant secretion of mucus.

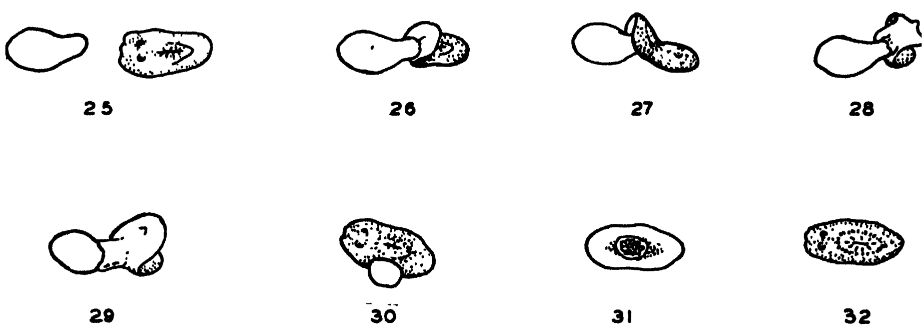
TEMPERATURE—The limits of toleration of Stylochi for high temperatures were tested by slowly heating five individuals in a beaker containing 300 cc. of sea water which was stirred constantly on a sand bath. Up to 40°C. all lived; at 41°C. two died and three lived; at 42°C. all died. Low temperatures were tested in an electric refrigerator where by shifting to different regions various temperatures could be maintained fairly constant for hours at a time. The worms were placed separately in ten 100 cc. beakers filled with sea water; a pair of beakers could thus be removed at

intervals. Individuals recovered after being kept at 1.0, 0.7°, and 0.5°C. for one hour or more but all those that reached 0.0°C. or below died. Larvae survived lower temperatures than adults. Some lived for more than an hour at —2.0°C.; about a twentieth of those subjected to —2.5°C. were alive, though the water about them contained ice crystals.

Adult *Eustylochus meridianalis* tolerate lower temperatures than *Stylochus inimicus.* At 9.16°C. to 11.3°C. the latter crumpled up and lost its attachment to the substratum while the former continued to crawl about and remained attached down to —1.0°C. Eustylochus adults lived in ice at —2.0°C.; larvae survived —1.0°C. Adult Eustylochus usually died when heated to 39.0°C.; e.g.—in one experiment 2 of 5 lived after five minutes at that temperature, but after ten minutes five others all died. At 40.0°C. all adults tested died. Eustylochus larvae survived temperatures as high as 44.0°C. for a short time and recovered.

In order to test the effects of temperature on egg-laying two lots of ten pairs of Stylochus in separate covered finger bowls were kept under different conditions from November 18 to 28. Lot 1 was kept in the laboratory where temperatures ranged from 8.3 to 25.7°C., average 18.7°C.; after ten days all "leeches" were alive, 12,800 eggs had been laid in three bowls. Lot 2 was kept on the north porch of the laboratory, where temperatures ranged from 3.3°C. to 21.9°C., average 13.9°C.; after ten days 13 were alive and 7 dead, no eggs had been laid.

FOOD AND FEEDING—*Stylochus inimicus* apparently feeds largely on oysters (Figs. 25-32). In the laboratory individuals which had not had food for some time ate the soft parts of barnacles and crepidulas, but did not eat shrimp or fish. On the other hand *Eustylochus meridianalis* readily ate barnacles and even killed Balanus to get food, but was never seen to enter a living oyster to feed on it, though it was given many opportunities to do so. Stylochi which had just been brought in from the field were teased apart in attempts to discover the nature of the foods eaten. Nothing was found but parts of oysters, except a very few small organisms, such as peridinians and



FIGS. 25-32. A Stylochus approaching (25) a piece of oyster, swallowing it (26-30), withdrawing its pharynx (31), and engorged (32).

diatoms, which were probably part of the food of the oysters eaten. Eustylochi kept without food from March 20 to April 2 decreased from an average length of 14.0 mm. to 10.5 mm. (25 percent) during the thirteen days. Stylochi kept without food from November 18 to March 5 decreased from an average length of 24.2 mm. to 16.6 mm. (30 percent).

BEHAVIOR—When placed in a rectangular glass dish containing sea water in a dark room adult Stylochi are generally negative to a horizontal beam of light of intensity of about 0.15 to 3.5 candle meters. Larvae were strongly positive under similar conditions. Adults appear to move without reference to currents. Swimming larvae are somewhat negatively rheotropic; e.g., in current moving at a rate of 10 mm. per second the larvae swam in an erratic course with many twistings and turnings, but only moved along with the current at a rate of about 8.8 mm. per second. The tentacles and brain of adults are not essential to photic and rheotic responses; animals respond more slowly but in much the same way after these organs are removed. Most individuals are strongly stereotropic and if dislodged will usually turn over repeatedly so as to keep the ventrum in contact with the substratum. The brooding responses when eggs are present have already been discussed. They are probably brought about by chemico-tactile stimuli.

ECOLOGY

Stylochus inimicus in its environmental relations requires food, which appears to consist largely of the fleshy parts of oysters; sea water in which salinity does not fall below about 6 0/00 and for as much as a fortnight remains above about 15 0/00 for the development of eggs; temperatures above about 10°C.; clean shells or other similar objects, which are not already occupied by annelids, crabs, alpheids, sponges, clams, snails, barnacles, or other animals, for shelter and the deposition of eggs. Such a complex of environmental conditions is most often found on oyster beds in comparatively warm climates. As oysters usually grow in estuaries where water is brackish and at times becomes too fresh for the reproduction, or even the life of Stylochus, there is at times antagonism between requirements for food and those for propagation. *Eustylochus meridianalis*, though it is often associated with Stylochus, lives in a somewhat different environment where acorn barnacles may constitute the chief food, where water may be fresher (0.6 ± 0/00) and temperatures lower. As would be expected Stylochus is found primarily on oyster beds along the southern coasts of Florida, on both the east and west coasts; Eustylochus is known to range from Maryland to Texas and is widely distributed on oyster beds, piles, isolated old shells, logs, and other similar situations.

DISTRIBUTION—Two methods were used in studying the distribution of polyclads in Apalachicola Bay and adjacent waters: (1) A measured bushel of tonged oysters and shells was carefully searched by Pearse, Wharton, Saw-

yer and Lane; nearly every living and dead shell was opened and scrutinized, inside and out—barnacles, crepidulas, mussels, etc.; all polyclads were counted, placed in a jar of sea water, and later measured in the laboratory; records were also kept of numbers of individuals (a) in or on clean oyster shells, (b) in living or recently dead oysters, and (c) those brooding clutches of eggs, and at times the number of eggs in clutches. (2) A fifth of a bushel of oysters was placed in a white enameled pail and covered with water. The pails were taken to the laboratory and allowed to stand for 24 or 48 hours, depending on temperature; the polyclads which came to the surface were removed, counted, and measured. When salinities were low those in pails were determined by titration with silver nitrate. From August 8 to November 19, 1935 the shells put into pails were those which had already been searched in examining bushels, in order to ascertain whether the bushel-searching methods were effective, but from November 25, 1935 to May 20, 1936 unexamined shells only were used for the pail survey method. Of course smaller polyclads, even swimming larvae, could be found than on the clean shells in the field. After much preliminary scouting fifteen stations (Fig. 33) which represented conditions on various types of oyster beds were selected for study, and were visited at least once each month after June 20, 1935. In the following list depths given are the means from which oysters were actually tonged or (Hile's Deep Bar only) dredged; s indicates surface; b, bottom:

1. Hile's Shallow Bar, near Indian Pass, an oyster bed planted with dredged oysters from East Hole and Cat Point in 1931-1932; mean depth 1.3 meters; salinity, s, 32.45-5.97, b, 34.41-5.97; temp., s, 25.6-12.0°C., b, 32.0-12.0°C.

2. Hile's Deep Bar; an artificial bed planted with dredged oysters from East Hole and Cat Point in 1931; depth 3.4 meters; salinity s, 33.88-2.34, b, 34.02-8.50; temp., s, 28.9-11.4°C, b, 28.9-10.6°C.

3. Picolyne Bar; a natural oyster bed which has been tonged for many years, but never dredged; depth 1.1 meters; salinity s, 33.75-2.74, b, 33.75-3.04; temp., s, 28.5-11.2°C., b, 32.3-11.6°C.

4. Lump off 11-Mile; a natural bed where oysters have long been tonged, but never dredged; depth 1.2 meters; salinity s, 32.28-1.60, b. 33.85-1.60; temp., s, 29.9-7.7°C., b, 31.1-7.7°C.

5. Big Bayou Bar; a bed in a lagoon on the north side of St. Vincent Island which contains some native oysters, but mostly planted with oysters from East Hole and Cat Point in 1933; depth 1.7 meters; salinity s, 30.07-2.31, b, 29.80-24.7; temp., s, 30.4-11.4°C., b, 30.4-11.4°C.

6. St. Vincent Bar, North End; a natural bar which has long been exploited by tongs, and since 1933 by dredges; depth 1.5 meters; salinity s, 32.46-0.40, b, 34.58-0.60; temp., s, 27.8-7.2°C., b, 31.4-4.2°C.

7. St. Vincent Bar, Middle; depth 1.4 meters; salinity s, 32.46-1.90, b, 33.35-1.90; temp., s, 28.3-8.1°C., b, 32.0-8.1°C.

8. St. Vincent Bar, South End; depth 1.4 meters; salinity, s, 32.47-1.60, b, 35.16-2.52; temp., s, 27.8-7.2°C., b, 29.9-7.2°C.

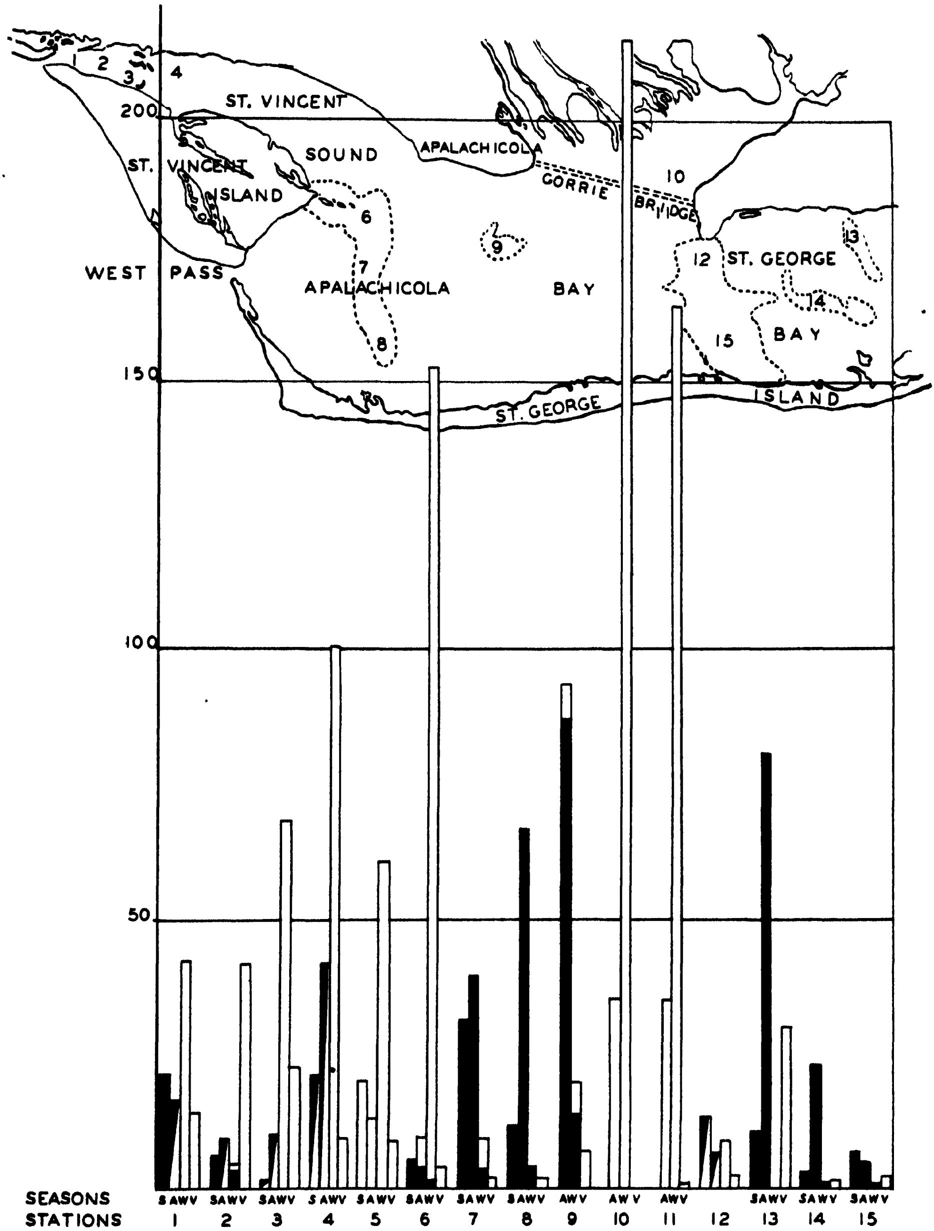


FIG. 33. Stations in Apalachicola Bay where monthly observations were made. Black indicates seasonal distribution of *Stylochus inimicus;* white, that of *Eustylochus meridianalis.* Seasons: *A*, autumn; September, October, November; *S*, summer; June, July, August; *V*, spring; March, April; *W*, winter; December, January, February. Based on Table 6.

9. Hagen's Flats; a natural bar which has been tonged and dredged; depth 1.8 meters; salinity s, 30.96-0.50, b, 31.14-2.20; temp., s, 24.4-9.2°C., b, 24.6-9.2°C.

10. East Bay; a natural oyster bed which has been tonged and, since 1933, dredged; depth 1.9 meters; salinity s, 20.19-0.00, b, 28,66-0.10; temp., s, 28.2-8.9°., b, 28.2-8.9°C.

11. Gorrie Bridge, East End; a natural bar which has been tonged and dredged; depth 1.6 meters; salinity s, 29.51-0.05, b, 29.37-0.05; temp., s, 28.4-9.6°C., b, 28.3-9.4°C.

12. Cat Point; a natural oyster bed which has been tonged and dredged; depth 1.6 meters; salinity s, 31.69-0.05, b, 31.92-0.05; temp., s, 26.7-8.9°C., b, 31.7-8.9°C.

13. Porter's Bar; a natural oyster bed which has been tonged and dredged; depth 1.6 meters; salinity s, 31.98-2.35, b, 31.98-3.96; temp., s, 23.9-8.6°C., b, 32.2-8.6°C.

14. Platform Bar; a natural oyster bed on which "leeches" were abundant in 1932; tonged and dredged; depth 1.6 meters; salinity s, 32.23-2.03, b, 32.23-3.23; temp., s, 23.9-8.9°C., b, 32.7-8.9°C.

15. East Hole; a natural bed, near St. George's Island, which has been tonged and dredged; depth 2.1 meters; salinity s, 31.98-2.23, b, 32.23-3.02; temp., s, 37.0-8.6°C., b, 32.2-8.6°C.

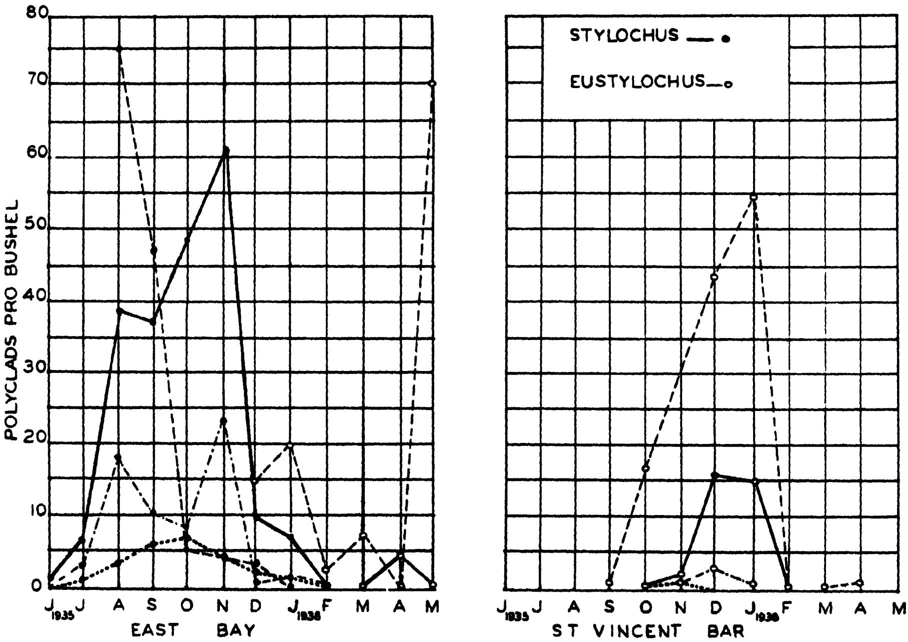


FIG. 34. Seasonal distribution of Stylochus and Eustylochus in the middle of St. Vincent Bar and in East Bay, showing numbers found in pails (- - - - -), in bushels (———), in live oysters (..........), and with eggs (-.-.-.-). Eustylochi taken in pails from East Bay are shown as numbers in one tenth of a bushel; those from St. Vincent Bar in number per bushel.

The numbers of Stylochus and Eustylochus at the fifteen stations studied is shown throughout a year in Figure 33 and Table 6.

TABLE 6. STYLOCHUS AND EUSTYLOCHUS; DISTRIBUTION BY SEASONS
JUNE, 1935 TO MAY, 1936
Figures indicate polyclads per bushel

<table>
<tr><th rowspan="3">Station</th><th colspan="2">SUMMER</th><th colspan="2">FALL</th><th colspan="2">WINTER</th><th colspan="2">SPRING</th></tr>
<tr><th colspan="2">June-August</th><th colspan="2">September-November</th><th colspan="2">December-February</th><th colspan="2">March-April</th></tr>
<tr><th>Stylochus</th><th>Eustylochus</th><th>Stylochus</th><th>Eustylochus</th><th>Stylochus</th><th>Eustylochus</th><th>Stylochus</th><th>Eustylochus</th></tr>
<tr><td>1. Hile's Shallow Bar</td><td>20.8</td><td>0</td><td colspan="2">15.8</td><td>5</td><td>37.9</td><td>0</td><td>13.9</td></tr>
<tr><td>2. Hile's Deep Bar</td><td>5.8</td><td>0</td><td colspan="2">8.6</td><td>2.7</td><td>0.8</td><td>0</td><td>40.3</td></tr>
<tr><td>3. Picolina</td><td colspan="2">0.8</td><td colspan="2">8.7</td><td>0</td><td>67.8</td><td>0</td><td>21.8</td></tr>
<tr><td>4. 11-mile Lump</td><td colspan="2">19.4</td><td colspan="2">41.5</td><td>0</td><td>100.3</td><td>0</td><td>9.4</td></tr>
<tr><td>5. Bayou</td><td>0</td><td>20</td><td>0</td><td>12.9</td><td>0</td><td>61.7</td><td>0</td><td>8.8</td></tr>
<tr><td>6. St. Vincent's N.</td><td>5.0</td><td>0</td><td>3.9</td><td>5.9</td><td>1.5</td><td>153.2</td><td>0</td><td>3.9</td></tr>
<tr><td>7. St. Vincent's M.</td><td>30.3</td><td>0</td><td>39.6</td><td>0</td><td>3.3</td><td>6.3</td><td>0</td><td>1.4</td></tr>
<tr><td>8. St. Vincent's S.</td><td>11.7</td><td>0</td><td>67.7</td><td>0</td><td>4</td><td>0</td><td>0</td><td>1.4</td></tr>
<tr><td>9. Hagen's Flats, inside</td><td>—</td><td>—</td><td>86.5</td><td>7.5</td><td>13.7</td><td>5.8</td><td>0</td><td>7</td></tr>
<tr><td>10. East Bay, bridge outside</td><td>—</td><td>—</td><td>0</td><td>35.7</td><td>0</td><td>216.4</td><td>0</td><td>0</td></tr>
<tr><td>11. East Bay, bridge</td><td>—</td><td>—</td><td>0</td><td>35.6</td><td>0</td><td>169.0</td><td>0</td><td>.3</td></tr>
<tr><td>12. Cat Point</td><td colspan="2">13.8</td><td colspan="2">6.3</td><td>0</td><td>9.8</td><td>0</td><td>2.8</td></tr>
<tr><td>13. Porter's Bar</td><td>10.5</td><td>0</td><td>81</td><td>0</td><td>2</td><td>0</td><td>0</td><td>30.6</td></tr>
<tr><td>14. Platform Bar</td><td>3.2</td><td>0</td><td>23.3</td><td>0</td><td>0.8</td><td>0.4</td><td>0</td><td>1.4</td></tr>
<tr><td>15. East Hole</td><td>7.7</td><td>0</td><td>5.5</td><td>0</td><td>0.5</td><td>0</td><td>0</td><td>2.4</td></tr>
</table>

Stylochus reached its maximum abundance in the fall of 1935; Eustylochus was most abundant in the winter of 1935-36 and decreased greatly after the freshet early in the spring of 1936. Eustylochus continued to lay eggs when brought into the laboratory throughout the winter and spring. In general, Stylochus flourished during warm weather where oyster beds grew in rather salty water; Eustylochus was more often found during colder parts of the year where barnacles were abundant alongshore, on oyster beds or elsewhere. These statements are general and were of course not absolutely supported by field evidence. For example, the greatest number of Stylochus ever found in one "tonged and searched" bushel was 204 in October on Hagen's Flats, where water is not as salty as on St. Vincent Bar. The greatest number of Eustylochus per bushel by the pail method was 1375 on March 16 on Green Point lump, which is east of any of the stations studied in routine surveys. Water there is generally quite saline.

In any one season conditions in a particular place may be favorable or unfavorable. The millions of pelagic larvae which polyclads produce enable them to invade every available habitat; once established, fortunate or un-

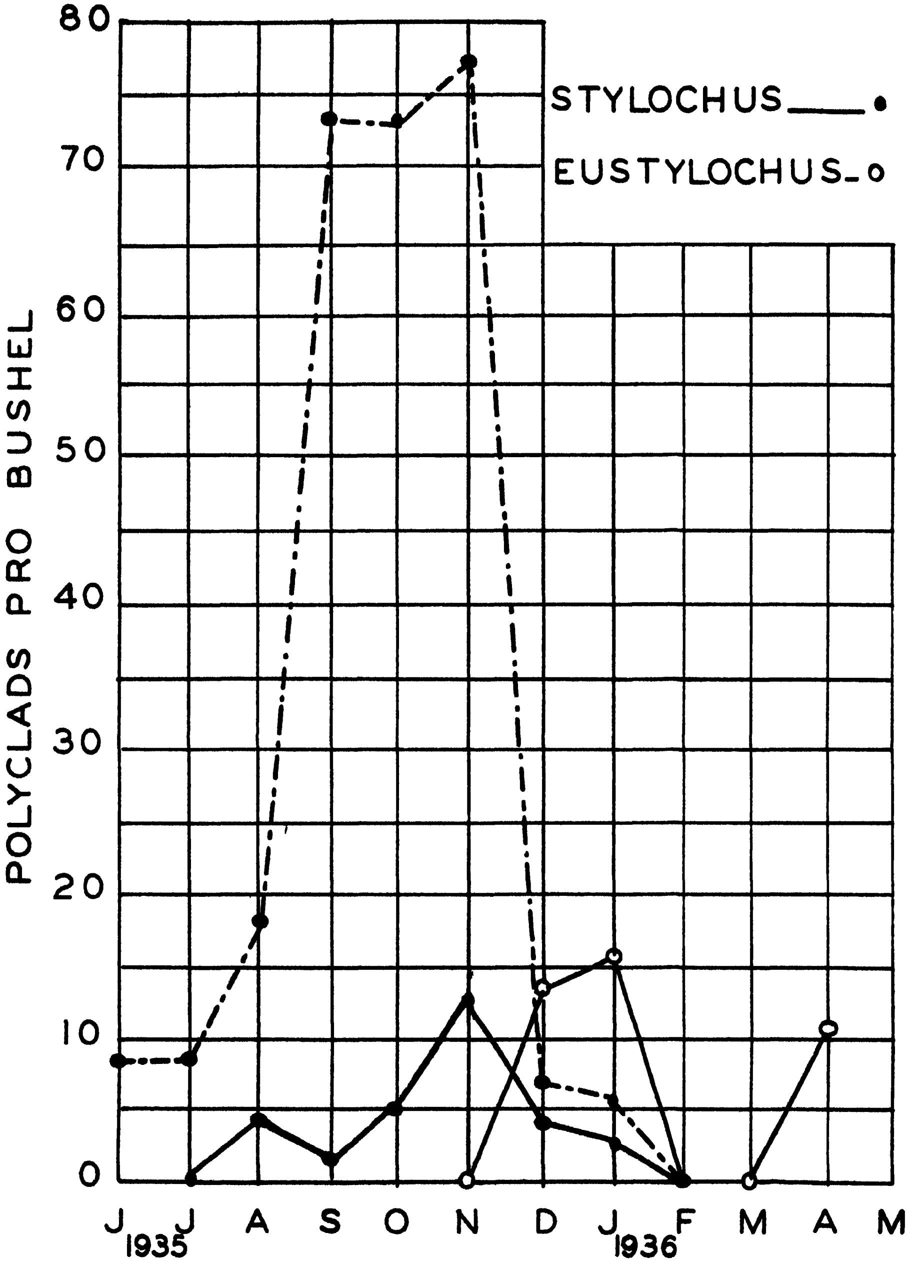


FIG. 35. Occurrence of Stylochus and Eutylochus per examined bushel, on the north (-.-.-) and south (———) ends of St. Vincent Bar.

fortunate combinations of winds, freshets, temperatures, and other environmental factors determine whether they perish, survive, or flourish. In 1932-1935 there were myriads of Stylochi on Porter's Bar; in 1935-36 there were not as many there as on Hagen's Flats and St. Vincent Bar.

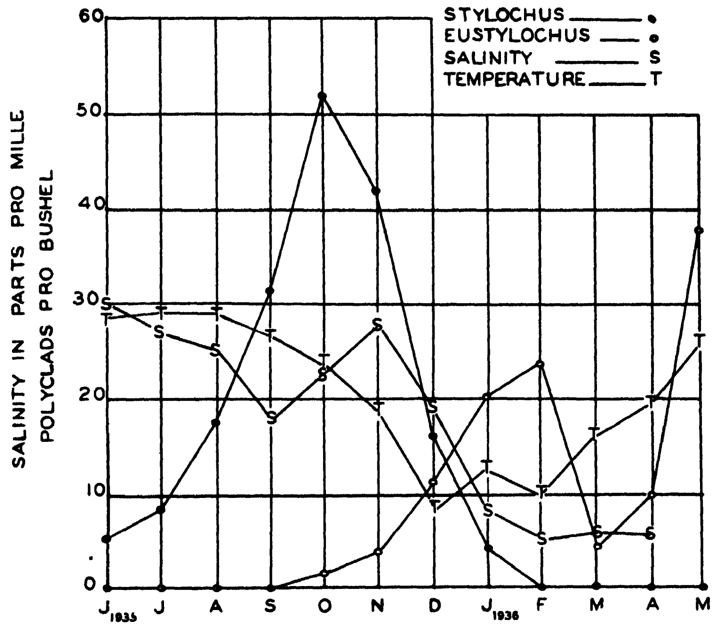


FIG. 36. Occurrence of *Stylochus inimicus* and *Eustylochus meridianalis* in relation to salinity and temperature during 1935 and 1936 in Apalachicola Bay.

FOODS—Polyclads appear to have become specialized for particular types of food: *Stylochoplana floridana* Pearse eats copepods and annelids: *Thysanozoon brochii* Grube commonly feeds on the ascidian, *Didemnum candidum* Savigny, which grows on the eel grass in St. Joe Bay. *Stylochus inimicus* apparently feeds on oysters, and seldom on anything else. In the laboratory Stylochi which had been kept for some time without food ate acorn barnacles and crepidulas as well as oysters, but refused the flesh of fish, and several species of snails and clams. On October 28 four freshly collected oysters were put in an aquarium where there were about 1,000 Stylochi in running sea water. Three days later 85 of the worms had entered and were devouring one oyster; the three other oysters contained 21, 50, 51 worms. Table 7 indicates that young, small oysters are more often eaten than large. The "partitions" (Fig. 37) built as a defense against "leeches" are particularly significant in the table.

TABLE 7. SHOWING ATTACKS OF TEN *Stylochus inimicus* ON FRESH OYSTERS FROM CAT POINT. STYLOCHI INTRODUCED ON SEPTEMBER 9; TWO LOST BEFORE SEPTEMBER 16, WHEN OYSTERS WERE EXAMINED

Size of oysters, mm.	No. of oysters, Sept. 9	Stylochi in living oysters	"Leech" partitions in shells	Oysters rotting	Oysters dead	Oysters normal
1–10.	177		8	4	46	131
11–20.	84	2	2		8	74
21–30	8		1	1	2	6
31–40.	5			1	1	4
41–50	1					1
51–60.	9					9
61–70	6	1				5
71–80	3					3
81–90	8	1		2	2	5
Total	301	4	11	8	59	238

In the field Stylochi were often found in living, dying, or recently dead oysters, but, though thousands of crepidulas, acorn barnacles, and mussels growing with and attached to oysters were examined, none was ever found in them. *Eustylochus meridianalis* in the laboratory killed and devoured barnacles, readily ate the soft parts of barnacles and oysters, but was never observed to enter a living oyster, though it was given many opportunities to do so. In the field it was found in barnacles and oysters which were gaping open but never in closed, apparently healthy oysters.

ENTRANCE OF STYLOCHUS INTO OYSTERS—Stylochus was observed to enter living oysters on several occasions. The worm crept slowly up and attempted to enter between the lobes of the mantle. The oyster usually closed quickly and "blew" the leech out in the resulting current of water, but the leech persisted and usually after several trials succeeded in entering. But the oyster did not give up the struggle against its enemy. It at once began to secrete a horny partition and thus attempted to seal the worm into its own shell. In two instances Stylochi were found completely covered over in that way, and other instances were probably observed when the worms had disintegrated so that they could not be positively identified. In cases under observation it required about two days to build a partition. Sometimes the invading worm crept over the first defense partition that the oyster secreted and the oyster then made another; or at times even as many as five partitions. During such a struggle the oyster's body was confined to a smaller and smaller space; probably also weakened and perhaps partly devoured. The defensive partitions are such a characteristic response to Stylochus attacks that oystermen in looking over shells on bars or oyster shell refuse heaps remark, "leeches have been here," when they find such a partition. An oyster which has been invaded by a Stylochus opens and closes more often than one which has not been entered.

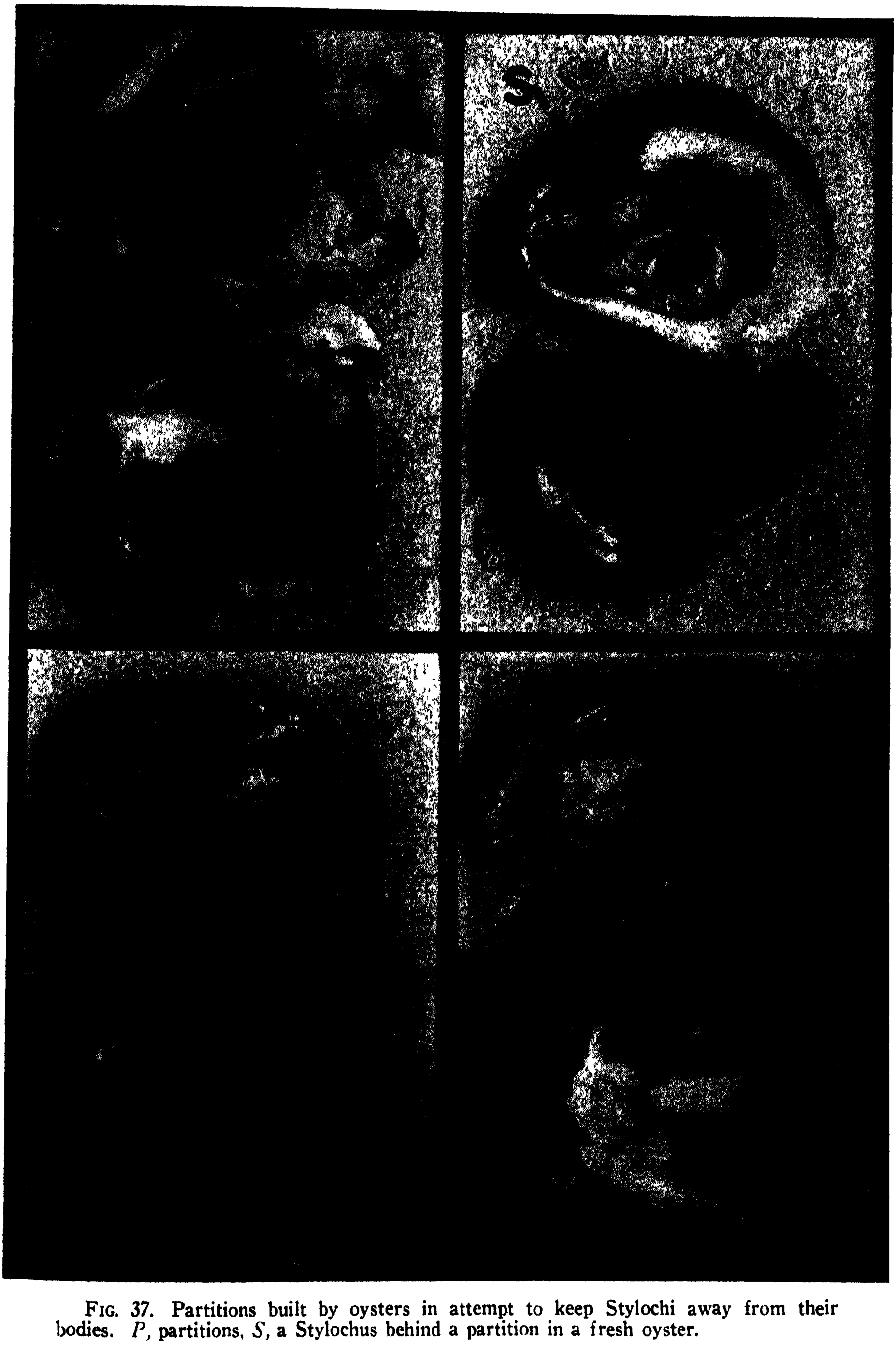


FIG. 37. Partitions built by oysters in attempt to keep Stylochi away from their bodies. *P*, partitions, *S*, a Stylochus behind a partition in a fresh oyster.

BREEDING—Any hard clean surface appears to be suitable for the reception of the irregular, single-layered egg masses of Stylochus and Eustylochus. The shells of molluscs are commonly used, but either worm will readily lay eggs on the sides of a glass dish. Temperature and salinity influence egg laying. When water is about half as saline as that in the open sea Stylochus lays few or no eggs. Egg laying is also inhibited by low temperatures. Therefore, an oyster "leech" may continue to live where it is not possible for it to reproduce. A Stylochus can move fast enough and lays a clutch of eggs quickly enough so that it could creep up several feet into the intertidal zone with a rising tide and leave eggs, but these would not survive as they have little ability to endure desiccation. However, Stylochi have a breeding period which extends over several months. During this time they appear to be ever ready to copulate and lay eggs when conditions are favorable, so it would be seldom that fresh water and low temperature would not be remitted for two or three weeks, so that eggs could be laid and hatched.

EFFECTS OF VARIATIONS IN ENVIRONMENT—*Stylochus inimicus* and *Eustylochus meridianalis* are members of complex societies which live on oyster beds. Perhaps it is correct to say that the latter belongs to the Balanus Society rather than the Ostrea Society, and that it spreads over oyster beds when conditions are particularly favorable. The plants and animals which form societies fluctuate in numbers greatly in different years and with changing seasons in any one year. The most apparent causes of fluctuations in Apalachicola Bay are changes in salinity and temperature. In the summer and autumn of 1936 the following plants and animals lived together on the oyster beds in the bay. In the list which follows *S* indicates salinity in grams per liter. Of course the list does not include all animals which occur in Apalachicola Bay and adjacent waters, but only those that were encountered on oyster beds or appeared to be significant in the study of oyster leeches. As the animals have been identified by specialists, their names are given with brief notes which may be of use to those who work in the region. Unless otherwise stated the notes refer to collections made during routine monthly visits to the fifteen oyster bars selected for study (p. 626).

LIST OF PLANTS AND ANIMALS

Observed on Oyster Bars in Apalachicola Bay

PROTOPHYTA

Ulva sp.

Sea lettuce was often encountered in the east end of Apalachicola Bay; on such bars as North Lump and Sugar Loaf.

Sargassum natans (L) Meyen

This alga was collected on June 6 on Platform Bar and on March 16 on North Lump.

Gracilaria confervoides (L) Grev.

This branching alga was common to abundant throughout the year on Platform Bar (S: Bl. 98-3.23), East Hole, Porter's Bar, North Lump, and Sugar Loaf. At times it constituted an obstacle to tonging and dredging operations.

Spirogyra sp.

Collected in East Bay February 6 (S: 0.1) after a freshet.

Enteromorpha intestinalis (L.) Link.

East Hole, December 30; S: 14.94.

Enteromorpha prolifera Agardh.

March 16; Sugar Loaf; S: 22.30.

PROTOZOA

Nematopsis ostrea Prytherch

Living oysters were sent to Dr. H. F. Prytherch from 11-mile Lump and Platform Bar on December 27 and December 30. Spores of this sporozoan parasite were found in the gills: from 400 to 25,000 per square centimeter. In 1934 Dr. Prytherch found this sporozoan in oysters collected in Apalachicola Bay from Bulkhead Bar. Oysters sent by the writers from Fernandina and Oslo on the east coast of Florida at the end of January were also found to contain spores by Dr. Prytherch.

PARAMECIUM, COLPODA, OXYTRICHA

On February 6 in pails of oyster shells collected from East Bay (S: 0.1) numerous ciliates collected at the surface.

PORIFERA

Cliona vastifica

The boring sponge was most commonly found attacking oysters in the parts of Apalachicola where salinities were high—Platform Bar, Porter's Bar, St. Vincent Bar, Hile's Deep Bed, Picolyne Bar. Sponges were not common in the bay.

COELENTERATA

Nemopsis bachei Agassiz

In tow nets at East Hole (S: 14.94) December 30; Picolyne Bar (S: 22.47) and Hile's Shallow Bed (S: 23.81), January 2; and Hagen's Flats (S: 17.24), January 9.

Physalia pelagica Bosc

The Portuguese-man-o'war was at times common on the beaches along the outlets but was never seen in Apalachicola Bay.

Stomolophus meleagris Agassiz

Rhizostomes were often swept into Apalachicola Bay on currents from the Gulf of Mexico.

Renilla reniformis (Pallas)

This stalked actinian was commonly in shrimp trawls in the Gulf of Mexico just off shore, but was not observed in Apalachicola Bay.

Paranthus rapiformis (Lesueur)

This anemone was common in the sandy shores of Indian Pass, and was the species often found on oyster shells in Apalachicola Bay where salinities were rather high, but specimens of the latter were too young to be identified with certainty.

Astrangia danae Edw. & Haime

This coral was found among tonged oysters on St. Vincent Bar and Platform Bar. No living specimens were found after the freshet in the winter of 1935-36.

CTENOPHORA

Mnemiopsis gardeni Agassiz

Ctenophores were captured in tow nets at various times and places: December 6, East Bay (S: 18.73), Hagen's Flats (S: 14.66); January 2, Big Bayou Bar (S: 19.76); January 9, East end of Gorrie Bridge (S: 14.45).

PLATYHELMINTHA

Stylochus inimicus Palombi

The oyster leech was distributed throughout Apalachicola Bay and adjacent areas until the freshets in January, February, and March destroyed it.

Stylochus floridanus Pearse

Seven specimens were collected during the summer from the oyster beds in Apalachicola Bay.

Eustylochus meridianalis Pearse

This polyclad is usually associated with barnacles, but is often found on oyster beds and eats oysters at times. It tolerates lower salinities and temperatures than local representatives of the genus Stylochus.

Hoploplana thaisana Pearse

This polyclad was found several times during the autumn. When crushed conchs (*Thais f. floridana* Conrad) were allowed to stand in dishes of sea water, the worms crept up around the edge.

Acerosita pellucida Pearse

Two specimens of this polyclad were found on St. Vincent Bar in June.

Oculoplana whartoni Pearse

This ribbon-like polyclad was found on oyster shells in Apalachicola Bay, and at Crystal River and St. Lucie, Florida.

Prosthiostomum lobatum Pearse

This slender, flat polyclad was found several times on oyster beds in Apalachicola Bay, and is widely distributed elsewhere in Florida on both east and west coasts.

Bucephalus gracilescens (Rudolphi)

This trematode was found infesting oysters on the beds in Apalachicola Bay: June 23, St. Vincent Bar; January 9, East Bay; January 22, Platform Bar and East Hole; January 24, Picolyne Bar; January 24, Big Bayou; February 14, Cat Point.

ANNELIDA

Phyllodoce n. sp.

This annelid was found on St. Vincent Bar during the summer and autumn when salinities were rather high, and in St. Joe Bay on October 24.

Harmothoe aculeata Andrews

This worm was found on Picolyne Bar on November 18; and in Crooked Island Sound on November 21.

Lepidametria commensalis Webster

This polynoid occurred on St. Vincent Bar during June and July, and was found on Picolyne Bar August 10.

Euphole globosa Winternitz

St. Vincent Bar, July 5, 1935.

Eusyllus sp.

St. Vincent Bar, June 5.

Autolytus n. sp.

St. Vincent Bar, September 26.

Podarke obscura Verrill

St. Vincent Bar, August 1.

Nereis limbata Ehlers

This was the commonest and most widely distributed polychaete on the oyster beds in Apalachicola Bay at all seasons (S: 34.74-0.05). It lived among oyster shells everywhere. At times it was found in live oysters, which built partitions in attempts to shut it out of the mantle cavity.

Nereis pelagica L.

This worm was not as common as the last and did not tolerate as low salinities, but regularly lived among oysters in Apalachicola Bay.

Marphysa acicularum Webster *brevibranchiata* Treadwell

Hile's Shallow Bed; July 11.

Glycera sp.

St. Vincent Bar, July 19.

Polydora sp.

This worm was twice found moving about in living oysters (December 3, St. Vincent Bar; March 30, Big Bayou Bar) and was commonly found in holes along the margins of the shells of living oysters. It apparently bores into the shell of the oyster and doubtless does some damage. Oysters often cover the worms over with secretions and thus imbed them in their shells. *Polydora ciliata* (Johnson) infests shells of oysters in New South Wales.

Chaetopterus variopedatus Revieri

In beaches at Indian Pass and on the flats in St. Joe Bay, but not found on the oyster beds in Apalachicola Bay.

Streblosoma verrilli Treadwell

Porter's Bar, December 30, March 4; St. Vincent Bar, June 5, July 5, July 19, December 27.

Eupomatus uncinatus (Phil.)

Commonly distributed throughout Apalachicola Bay on oyster shells and other suitable objects.

Thalassema mellita Conn.

St. Vincent Bar, July 5.

ROTIFERA

Rotifers were taken in tow nets on Picolyne Bar, January 2, and in East Bay, March 6.

ECHINODERMATA

Hemipholis elongata (Say)

The young of this ophiuroid were the only echinoderms found on the oyster beds in Apalachicola Bay, but in St. Joe Bay and Crooked Island Sound, only a few miles to the east, there were ten other species. Hemipholis was not found where the lowest salinities obtained.

ARTHROPODA

CRUSTACEA

COPEPODIDA

Echinostoma curticorne Boeck

This crustacean came to the surface in a pail of oyster shells collected on St. Vincent Bar, June 12.

Mytilicola intestinalis Steuer

A specimen of this copepod was taken from a living oyster which was collected on Hagen's Flats December 5. Dr. C. B. Wilson, who identified it, writes that it has not been taken in America before.

CIRRIPEDIDA

Balanus eburneus Gould

This acorn barnacle was the commonest one throughout Apalachicola Bay at all seasons (S: 33.27-0.05). At the end of March many individuals were with eggs. Though this barnacle was most abundant on oyster shells in brackish water, most of the small individuals in East Bay died after the freshets in February and March, when salinities went as low as 0.05 0/00, but some large individuals survived.

Balanus improvisus Darwin

This barnacle was not as common in Apalachicola Bay as the last, but was also widely distributed.

AMPHIPODIDA

Gitanopsis tortugae Showmaker

A small amphipod which was present throughout Apalachicola Bay from Platform Bar to Indian Pass during the summer, but was not seen after the freshets in the winter.

Melita nitida Smith

This amphipod was distributed throughout Apalachicola Bay on the oyster beds. It survived the winter freshets and in April persisted in salinities as low as 0.05 0/00 in East Bay.

Carinogammarus mucronatus (Say)

This amphipod appeared in East Bay in February after freshets and during March and April spread to St. Vincent, Porter's, Platform, and East Hole Bars.

Grubia compta (Smith)

Found in the east end of Apalachicola Bay, East Hole, Platform Bar, and Cat Point from June to late in January; also in Crooked Island Sound, January 22.

Corophium simile Shoemaker

East Bay; April 13, (S: 0.05).

Corophium acherusicum Costa

11-mile Lump; November 19.

Grandidierella megnae (Giles)

Distributed throughout Apalachicola Bay, at times in very low salinities, from July to April.

Caprella acutifrons Latreille

Platform Bar; June 6.

Caprella linearis L.

St. Vincent Bar, September 26; St. Joe Bay, March 11.

ISOPODIDA

Leptochelia dubia (Kr)

Cat Point, Porter's Bar; January 22; Porter's Bar (S: 12.73), East Hole (S: 3.02), April 15; St. Vincent Bar (S: 3.20), April 17. In the eastern end of Apalachicola Bay this isopod was common August to April.

Exoxphaeroma faxoni Richardson

Platform Bar, June 6; East Hole, January 22.

Erichsonella attenuata (Harger)

Platform Bar, June 6.

Erichsonella filiformis (Say)

East Hole, January 22.

Pseudione curtata Richardson

In the gill cavity of *Petrolisthes armatus* (Gibbes) throughout the summer.

DECAPODIDA

Palaemonetes vulgaris (Say)

Platform Bar, Porter's Bar, June 6; St. Vincent Bar, July 2.

Palaemonetes carolinus Stimpson

Cat Point; August 27.

Penaeus setiferus (L)

Common at certain seasons in Apalachicola Bay, especially in spring, and caught in trawls.

Crangon armillatus (M. Edw.)

Distributed on oyster beds throughout Apalachicola Bay; June to April.

Petrolisthes armatus (Gibbes)

This porcellanid was common among oysters on the beds in Apalachicola Bay during the summer and autumn, but was killed out by the winter freshets and none was seen after January 24.

Paguristes puncticeps Milne-Edwards

This large hermit crab continually wandered over the oyster beds and beaches of Apalachicola Bay, but on some of the former it succumbed to the winter freshets.

Hepatus epitheliticus (L.)

Hile's Deep Bed, July 11.

Callinectes sapidus Rathbun

The blue crab is common throughout Appalachicola Bay and persisting in salinities as low as 0.05 0/00; in winter it is buried in the bottoms and hard to find. Females with eggs were observed March 30.

Hexapanopeus augustifrons (Benedict & Rathbun)

Platform Bar, June 6.

Panopeus herbstii stimpsoni Rathbun

This crab was fairly common on the oyster beds in Apalachicola Bay, from June until the freshets in the winter killed it. None was seen on the beds after January 9.

Eurypanopeus depressus (Smith)

This little xanthid crab was abundant at all seasons throughout Apalachicola Bay and persisted on the oyster beds when salinities fell as low as 0.05 0/00.

Eurypanopeus dissimilis Benedict & Rathbun

Platform Bar: June 6.

Menippe mercenaria Say

The stone crab was common on oyster bars and alongshore in Apalachicola Bay. It persisted in salinities as low as 5.9 0/00.

Pinnotheres maculatus Say

Common in the wing shell, *Atrina rigida* Dillwyn, in Apalachicola Bay throughout the summer and until the host was killed by fresh water.

Pinnotheres moseri Rathbun

Hile's Deep Bed: November 19: one specimen was found in *Ostrea virginica* Gmelin.

Pinnotheres ostreum Say

On the east coast of Florida at Fernandina and Eau Gaillie, this crab was abundant in oysters: but at Oslo and St. Lucie it was rare, and was never seen by the writers on the west coast in or near Apalachicola Bay.

Pinnixa sayana Stimpson

One crab was found in the sand at Indian Pass, where Chaetopterus tubes were common; November 21.

Ocypode albicans Bosc

The ghost crab was common on the sandy beaches about Apalachicola Bay. In winter it was not active, but remained in the burrows.

ARACHNIDEA

ACARANIDA

Halacarid mites were taken on St. Vincent Bar, August 7; Picolyne Bar, August 21; in East Bay, January 9; and on Hagen's Flats, April 13.

ORIBATID MITE

Hagen's Flats, April 13, S: 0.5.

INSECTEA

Enallagma sp.

At east end of Gorrie Bridge, Apalachicola Bay, February 6, S: 0.6 nymph.

Hydroporus sp.

East Bay, February 6, S: 0.1; April 13, S: 0.05.

Helodid beetle larva

East Bay; February 6; S: 0.05.

Rhagovelia sp.

One female was collected at Cat Point August 27, S: 15.30-21.73.

Culex restuans Theobald

One larva was captured in East Bay, February 6, S: 0.1-0.2.

Chironomus sp.

The larvae of this chironomid were common in East Bay February 6 to April 14, S: 0.05-2.39; and at Cat Point, April 15, S: 3.63.

Palkomyia sp.

Two larvae were taken in East Bay, March 6, S: 2.36.

Protenthes culiciformis L.

Larvae were collected among living oysters in East Bay, April 13, S: 0.05.

Orthocladius sp.

Two larvae were collected among living oysters in East Bay, April 13, S: 0.05.

MOLLUSCA

AMPHINEUREA

Acanthochites spiculosa Rue

This chiton was common in Crooked Island Sound and St. Joe Bay, but was collected only in the eastern end of Apalachicola Bay, on Porter's Bar, and East Hole Bar.

PELECYPODEA

Arca transversa Say

A few were taken on St. Vincent Bar throughout the summer.

Noetia ponderosa Say

St. Vincent Bar, June 12; Hile's Shallow Bed, July 11.

Atrina rigida Dillwyn

A few were collected on St. Vincent Bar, until all were killed by the winter freshets; Porter's Bar, August 9, December 30.

Ostrea virginica Gmelin

With the next species on bars throughout Apalachicola Bay; many died after the winter freshets, especially young individuals; those which had lived nearest the mouth of the river (East Bay) appeared to tolerate fresh water better than those (St. Vincent, Platform) nearest the open sea.

Ostrea equestris Say

With the preceding species throughout Apalachicola Bay, but generally in shallow water.

Lima hians Gmelin

St. Vincent Bar, June 5, July 2, 11; Hile's Shallow Bed, July 11.

Anomia simplex d'Orbigny

Common in St. Joe Bay and Crooked Island Sound; rare in east end of Apalachicola Bay.

Brachidontes recurvus Rafinesque

This mussel flourished throughout Apalachicola Bay and was abundant where water was rather fresh. After the freshets of the winter and spring of 1936, it showed little or no mortality in salinities as low as 0.05 0/00. If often grew in great clumps on oysters.

Brachidontes exusutus L.

St. Vincent Bar, September 26; Crooked Island Sound, November 21.

Lithophaga bisulcata d'Orbigny

The "date shell" borer was found during the summer in oyster shells on St. Vincent and Porter's Bars. It bored in the shells of living oysters, but was not as common as Martesia.

Pinctada radiata Leach

This clam was taken June 5 and 14 on St. Vincent Bar.

Chama macerophylla Gmelin

St. Vincent Bar, June 12; Hile's Shallow Bar, July 11.

Trachycardium muricatum L.

St. Vincent Bar, June 3; Hile's Shallow Bar, July 11.

Chione cancellata L.

St. Vincent Bar, June 5, July 11; Hile's Shallow Bed, July 11; Hile's Deep Bed, March 2; Crooked Island Sound, November 21.

Venus mercenaria L.

St. Vincent Bar, June 14; Hagen's Flats; April 13, S:2.63.

Semele proficula Pult

St. Vincent Bar, June 5, 12; Hile's Shallow Bed, July 11.

Corbula blattiana C. B. Adams

St. Vincent Bar, June 25, July 2, 19; Hile's Shallow Bed, July 11.

Martesia cuneimeris Say

This little pholid bored into the shells of living oysters on most of the bars in the more saline waters of Apalachicola Bay. It was recorded from the following bars: St. Vincent, Paradise, Platform, Porter's, Hile's Deep, Hile's Shallow, Cat Point, Big Bayou, 11-mile, Picolyne, North Lump, and Sugar Loaf. Often the burrows of the clams penetrated completely through the shell and were sealed over by the oyster's mantle on the inside. This borer was killed by the freshets on St. Vincent Bar.

GASTROPODEA

Diadora alternata Say

St. Vincent Bar, June 12, 25, July 2; common in St. Joe Bay.

Turbonilla sp.

St. Vincent Bar, September 26.

Odiostomia impressa Say

St. Vincent Bar, August 1, September 26.

Polineces duplicata Say

St. Vincent Bar, June 12, October 10; Hile's Deep Bed, January 24; Crooked Island Sound, February 10.

Crepidula plana Say

This flat snail was abundant on old shells and those of living oysters in Apalachicola Bay. It was not found where waters were of low salinity (East Bay) and was killed in many places by the freshets in the winter and spring of 1936. It was with eggs on June 7 on St. Vincent Bar and continued to produce eggs until autumn.

Crepidula formicata L.

St. Vincent Bar, August 1, September 26; Crooked Island Sound, November 21; St. Joe Bay, March 26.

Selia adamsii H. C. Lea

St. Vincent Bar; August 1, September 26.

Cerithium floridanum Morch

St. Vincent Bar, June 7; Platform Bar, June 6, August 20; Hile's Shallow Bed, July 11; Picolyne Bar, August 21.

Eupleura caudata sulcidentata Dall

Green Point Lump, March 16; Crooked Island Sound, November 21; Porter's Bar, April 15.

Thais floridana floridana Conrad

This oyster-destroying conch was common on St. Vincent and Hile's Deep and Shallow Bars, but was rare (Picolyne) or absent elsewhere. It was depositing egg capsules during all of June and at least until July 11.

Anachis obsea ostreicola Melv.

This little snail was often abundant among shells on the oyster bars throughout Apalachicola Bay. It persisted in salinities as low as 0.6 0/00.

Mitrella lunata Say

Picolyne Bar, August 10.

NUDIBRANCHS

Several species of nudibranchs were collected on St. Vincent Bar, Porter's Bar, and Cat Point, June 5 to September 26. Representatives of these have been deposited in the United States National Museum, but none have been identified.

TUNICATA

Molgula occidentalis Traustedt

This asidian was not uncommon during the summer on the oyster bars in the saltier area of Apalachicola Bay, but it never attained large size as in St. Joe Bay and Crooked Island Sound.

CHORDATA

PISCEA

Felichthys felis (L.)

The gaff-topsail catfish was common throughout Apalachicola Bay and in the mouth of the river. On the oyster bars small schools often gathered beside a boat while oysters were being examined, and snatched up the small animals that were thrown overboard.

Leptocephalus conger (L.)

Leptocephalid larvae were taken in tow nets in Apalachicola Bay at the following stations: (February 4-15, 1936): 11-mile Lump, Picolyne Bar, Hile's Shallow Bed, East end of Gorrie Bridge, Cat Point, St. Vincent Bar.

Bascanichthys scuticaris (Goode & Bean)

Snake eel; St. Vincent Bar; April 7, S: 2.93; a specimen about 50 mm. long tonged from bottom with oysters.

Brevoortia tyramus (Latrobe)

Young were taken in tow nets; Porter's Bar, February 14; Hagen's Flats, April 13, S: 2.63; Cat Point, April 15, S: 3.63; St. Vincent Bar, April 14.

Anchoviella mitchelli (Cub. & Valen.)

Young in tow net; Porter's Bar, February 14.

Syngathus floridae (Fordan & Gilbert)

Platform Bar, July 1; common in St. Joe Bay.

Mugil cephalus L.

Common in Apalachicola Bay.

Trichonotus carolinus (L.)

Pompano often leaped near the boat over the oyster bars in Apalachicola Bay during the summer.

Lagodon rhomboides (L.)

Young pinfish in tow nets; east end of Gorrie Bridge, February 6.

Leiostomus xanthurus Lacepede

Young spot in tow net; east end of Gorrie Bridge, February 6; Porter's Bar, February 14.

Micropogon undatus (L.)

Young croakers in tow net, east end of Gorrie Bridge, February 6; Porter's Bar, February 14; Cat Point, April 16. S: 2.29.

Pogonias cromis (L.)

Schools of sea drum enter Apalachicola Bay and do damage on oyster beds. During June, 1935 a number were caught off the docks at the mouth of the Apalachicola River.

Microgobius thalassimis Jordan & Gilbert

Young in tow net; Porter's Bar, February 14.

Gobionellus hastatus (Girard)

Cat Point, tow net; April 15, S: 2.29.

Gobiosoma bosci Lacepede

The naked goby commonly lived in old oyster shells in Apalachicola Bay and St. Joe Bay. It was observed with eggs and young July 19, April 17, St. Vincent Bar, April 13, East end of Gorrie Bridge; April 15, East Hole, Cat Point. Salinities as low as 0.05 were tolerated.

Opsanus tau (L.)

The toadfish was commonly found in oyster shells in the saltier parts (S: 4.59) of Apalachicola Bay. On May 16 one was observed guarding eggs on Paradise Flats.

Gobiesox strumosus Cope

Clingfishes were common in oyster shells in the saltier parts (S: 1.30 ±) of Apalachicola Bay and St. Joe Bay. Individuals guarding clutches of eggs and newly hatched young on March 30 on Hile's Deep and Shallow Beds.

Hypsoblennius hentz (Lesueur)

This little blenny was common in oyster shells on the bars in Apalachicola Bay and St. Joe Bay. It did not endure low salinities as well as Gobiosoma.

Urophycis sp.

A young hake was caught in a tow net on Porter's Bar, February 14.

REPTILEA

Caretta caretta (L.)

Loggerhead turtles were seen at times during the summer over the oyster bars in Apalachicola Bay.

Malaclemys macrospilota (W. P. Hay)

Diamond-back turtles live in the salt marshes near Indian Pass and there are associated with oysters on shallow, or "Coon," bars.

AVEA

Various birds frequented Apalachicola Bay. In summer the commoner species were pelican, cormorant, common tern, leat tern, royal tern, Caspian tern, and laughing gull. In winter there were many herring gulls and broad-bill ducks. At times cuban plovers, skimmers, oyster catchers, and other shore birds were common. In the bayous tributary to the bay were herons.

MAMMALEA

Tursiops truncatus (Montague)

Schools of porpoises were seen almost daily, feeding along the oyster bars in Apalachicola Bay and at Indian Pass.

In St. Joe Bay, only ten miles from Apalachicola Bay, and in Crooked Island Sound, 35 miles away (where fresh water never enters in large quantities, large flats of eel grass exist, and there is a considerable body of deep water), the fauna is quite different. Animals and plants are common which have not been seen in, and are probably absent from, Apalachicola Bay. Among these may be mentioned:

Algae: *Acetabularia crenulata* Lebour, *Dasycladus clavaeformis* (Roth.) Ag., *Batophora oerstedi* Ag.

Eelgrass: *Zostera marina* L.

Polycladidida: *Discocelis grisea* Pearse, *Stylochoplana floridana* Pearse, *Conjugouterus parvus* Pearse, *Leptoplana variabilis* Girard, *Thysanozoon brocchii* Grube, *Pseudoceros maculosus* Pearse, *Oligogoclado floridanus* Pearse.

Bryozoa: *Bugula neretins* L.

Echinodermata: *Astropecten articularis* (Say), *Lucidia clathrata* (Say), *Echinaster spinulosus* Verrill, *Ophiothrix angulata poecila* H. L. Clark, *Ophioderma brevispinum* (Say), *Lytechinus variegatus carolinus* (A. Agassiz), *Mellita quinquiesperforata* (Leske), *Moira atrops* Lamarck, *Plagiobrissus grandis* (Gmelin), *Leptosynapta multigranulata* H. L. Clark.

Crustaceae: *Peltogaster* sp. on *Pagurus; Leucothoe spinicarpa* (Albidg.) in Molgula and Styela: *Melita fresneldii* (And.), *Elasmopus posillimanus* Bate, *Polycheira antarctica* (Stebbing), *Paracerceis caudata* (Say in Didemnum and Styela, *Ligyda exotica* (Roux), *Peneus braziliensis* Latreille, *Trachypeneus constrictus* Stimpson, *Eusicyonia laevigata* (Stimpson), *Tozeuma carolinensis* Kingsley, *Crangon packardii* Kingsley, *Conchedytes domestica* (Gibbes), *Pagurus longicarpus* Say, *P. bonairensis* Schmitt, *Portunus spinimanus* Latreille, *Panopeus americanus* Saussure, *Neopanope texana sayi* (Smith) in Styela, *Pinnixa cylindrica* (Say) in Pecten, *Sesarma cinera* Say, *Uca minax* (Le Conte), *Pelia mutica* (Gibbes) in Molgula, *Podochela riisei* Stimpson.

Arachnidea: *Limulus polyphemus* (L.) breeding March 26, 1936.

Insectea: a caddis-fly larva in a spun tube.

Pelecypods: *Pecten gibbus* (L.), *Modiolaria lateralis* Say, *Cardita floridana* Conrad, *Teredo bartschi* Clapp.

Gastropodea: *Calliostoma j. jujubinum* Gmelin, *Cerethium muscarum* Say, *Murex rufus sallianus* A. Adams, *Thais undata* Lamarck, *Tritonalia cellulosa* Conrad, *Nassa vibex* Say, *Busycon p. perversum* L., *Fasciolaria distans* Lamarck, *Tethys protea* Rang, *Cavolina longirostris* Blainville, *Urosalpinx perrugatus* Conrad, *Conus pealii* Green, *Murex rufus* Lamarck, *Turbo castaneus* Gmelin.

Cephalopodea: *Octopus vulgaris* Lamarck.

Enteropneusta: *Dolichoglossus kowalevski* (A. Agassiz).

Tunicates: *Amaroucium bermudae* Van Name, *Didemnum candidum* Savigny, *Styela plicata* Lesueur, *Molgula occidentalis* Traustedt, *Distaplia bermudensis* Van Name, *Diplosoma macdonaldi* Herdman *Tridide mnum* sp.

Fishes: *Hippocampus zosterae* Jordan & Gilbert, *Chilomycterus schaepfi* (Walbaum).

When in the first week in January 1935 freshets in Georgia caused the Apalachicola River to discharge fresh water into Apalachicola Bay, many animals which had survived the low temperatures disappeared. *Petrolisthes*

armatus (Gibbes) had been abundant but was gone completely by the end of January. On the other hand *Carinogammarus mucronatus* (Say) appeared first in East Bay on February 6 and by April 15 had spread over the whole of the east end of Apalachicola Bay (Porter's Bar, Platform Bar, East Hole). Many oysters and barnacles died; the former largely where water previously had been fairly saline (St. Vincent Bar), the latter where water had been fairly fresh (East Bay). Among the types which tolerated fresh water best the following may be mentioned: Eurypanopeus, Nereis, Carinogammarus, Gobiosoma, Gobiesox, Balanus, Ostrea, and Eustylochus.

RELATIONS OF OYSTERS TO ANIMALS ASSOCIATED WITH THEM—Certain of the animals which live on oyster beds unquestionably injure oysters. Among these are boring sponges; oyster "leeches"; polychaete worms; carnivorous gastropods, or conchs; boring clams; certain crabs; and fishes such as the drum. Others are not injurious to oysters; they are commensals or more or less without definite relations. Some animals do not attack oysters directly but injure them by competing for space to live and food—sponges, barnacles, mussels, ascidians, etc. Any change in environment may upset the established balance in a society and perhaps cause one type to decrease and another to increase. A certain societal complex goes with oyster "leeches." Along the coast of Florida from Apalachicola Bay to Indian River *Stylochus inimicus* is often common and the little oyster crab, *Pinnotheres ostreum*, is rare or absent. On the east coast north of Indian River the oyster crab is common. This animal probably does an oyster in which it lives little or no injury. The writers have had their attention fixed on polyclad worms in relation to oysters, but have incidentally noticed that in certain areas in Apalachicola Bay (St. Vincent Bar, Hile's Shallow Bed) conchs, chiefly *Thais f. floridana* Conrad, often kill oysters, but on other oyster beds (Porter's Bar, East Hole), where "leeches" are fairly common, these molluscs are rare or absent. All oyster pests do not flourish under the same conditions. Each species has its own peculiar environmental complex in which it is at its best. The little porcellanid crab, *Petrolisthes armatus* (Gibbes), probably does no harm to oysters, though it is often abundant on the bars in Apalachicola Bay. It appears to flourish under about the same condition as the oyster "leech," *Stylochus inimicus,* and, as it is more easily discovered, may be used as an indicator of conditions favorable for "leeches."

CONTROL OF OYSTER "LEECHES"

Perhaps the best way to kill Stylochus is to inundate oyster beds with fresh water. After the freshets in the winter and spring of 1936 not an oyster "leech" could be found in Apalachicola Bay. Perhaps in the future it may be possible and financially expedient to control oyster "leeches." There is little hope of exterminating the worms by chemicals, as they tolerate rather high concentrations of injurious substances. Expense would make

such measures inexpedient and oysters as well as pests would perhaps be killed.

Attempts were made to feed Stylochi to fishes kept in dishes in the laboratory. In this way four fishes which commonly occurred on oyster bars were tested; toadfish, sea robin, a goby (*Gobiosoma bosci*), and a blenny (*Hypsoblennius hentz*). Only the blenny ate Stylochi. One fish ate 4.5 large worms in four days.

INJURY TO OYSTERS BY "LEECHES"

There is no question that *Stylochus inimicus* enters, devours, and destroys oysters. The oyster fights the worm, as has been described (p. 632). The worm is present in living oysters continually (Fig. 37). Certain persons who visited Porter's Bar in Apalachicola in 1932-1933 when the oysters were dying rapidly maintain that Stylochus was solely responsible for the extermination of oysters; others who worked on the bar at that time say that many oysters died before they were attacked by "leeches," and that Stylochus was only a contributing cause of mortality. On all the oyster beds in Apalachicola Bay polychaete worms are continually making holes about the margins of the shells of living oysters; sporozoans are present in the bodies of oysters; conchs devour many oysters in certain areas; boring clams and sponges make holes in oyster shells; floods of fresh water may kill off considerable number of oysters; low temperature and high winds at times do great injury. There are so many things present in the bay at all times which may kill oysters that it is difficult to say that one of them is wholly responsible. Our observations make it appear that Eustylochus does not attack living oysters, but preys on barnacles and at times enters and eats oysters that are sick or dying.

It has been suggested that the cleaning of grounds and the careful planting of vigorous stock of carefully culled oysters would eliminate the oyster leech pest. There is unquestionably much to be done in Apalachicola Bay, and on the whole Florida coast where Stylochus occurs, for the improvement of methods of oystering. Careful preparation of beds, planting, and harvesting would doubtless result in better oysters and increased production, but would not eliminate Stylochus. Each worm may lay 20,000 eggs, which can hatch into swimming larvae that are carried everywhere by tidal currents. A "leech" may grow from egg to maturity in a couple of months. It is therefore possible for the most carefully prepared bed to become infested in a season when salinities and temperatures are high.

DISCUSSION

PREDATOR OR PARASITE—There is some question in the minds of many students of polyclads as to whether *Stylochus inimicus* Palombi should be called a parasite or not. Palombi (1931) argues that it is merely a commen-

sal. Roughley (1935) states that *Leptoplana australis* (Schmarda), which feeds on oysters in the Australian region, does not kill oysters but enters dead or dying individuals. He looks upon the worm as a scavenger. None could be induced to enter normal oysters in auaria. Bock (1925) affirms that *Stylochus ferox* Bock destroys young oysters along the coast of Japan. He looks upon the worm as a predator. On the coast of Florida there is no doubt that *Stylochus inimicus* enters living oysters, gradually devours their soft parts, and finally kills them.

Small animals which have intimate relations with larger animals, called hosts, are usually classified by zoologists under three groups: (1) Commensals live in or on their hosts without benefitting them. They may obtain food, shelter, or other benefits from their hosts or they may merely use the host as they would any other similar object. The crustaceans that live in the tubes or annelid worms and the little crabs that commonly dwell in oysters are examples of commensals. (2) Symbionts live with hosts which they benefit, and in return receive something from their hosts. A bird which sits on the back of a cow and picks off insects or ticks thus obtains food and frees its hosts of injurious parasites. (3) Parasites injure their hosts, and usually do so without causing death. A hookworm may cause anemia in its host. It often shows a tendency to attack only one species or one group of hosts; it is adapted to the temperatures, chemical characteristics, and other peculiarities of the host. A mosquito feeds only on homeothermic animals and will at times attempt to insert its proboscis into almost any warm object. A beef tapeworm will not live in any definite host except man, not even in anthropoid apes, and requires cattle for its secondary host; it has lost its enteron completely and must live within a host during all active stages in its life cycle. Yet a beef tapeworm rarely is even a contributing cause of the death of its host. Hosts generally have some degree of tolerance for their parasites (Herms 1932) and parasites, while they injure their hosts, seldom completely eliminate the sources of their benefits. This is adaptation.

Stylochus inimicus does not differ anatomically from nearly related free-swimming predaceous polyclads. It shows some adaptation to oysters in that it seldom feeds on anything else. On the other hand, oysters attempt to prevent the worms from entering and often enclose them within shell substances when they do enter. The worms if successful in their attack gradually devour and kill the oysters. Stylochus is properly to be looked upon as a predaceous animal which may in time become a parasite of oysters but has not as yet become adapted enough to be called one.

STRENGTH AND WEAKNESS OF STYLOCHUS—On the whole *Stylochus inimicus* is a hardy animal. In common with many other marine animals it can tolerate low oxygen (p. 620), withstand poisonous substances in rather high concentrations (p. 623), and endure prolonged starvation (p. 617). Its weaknesses are inability to remain active and alive (a) at low temperatures and (b) in low salinities. In its tolerance of such extremes it is less hardy

than its associate on oyster beds, *Eustylochus meridianalis.* Oysters are sensitive to temperature changes (Hopkins 1931). They tend to open when temperatures rise and close when there is a decrease. Above 20°C. they may feed about 20 hours daily, but do not feed at all below 4°C. (Nelson 1928). Galtsoff (1928) shows that feeding of oysters does not take place below 5°C. and often stops at 6-7°C. Spawning begins at about 20°C. (Nelson 1928). Stylochus is active between 12°C. and 34°C. It therefore cannot migrate far north on the Atlantic Coast. Up to the present it has been reported only along the Florida coast from Pensacola Bay on the west to Indian River on the east. It cannot tolerate salinities below 6 0/00 and does not lay eggs when they are below about 15 0/00. At summer temperature eggs require about eleven days for the development of a pelagic, swimming larva. These facts indicate that the most promising lines of attack and perhaps ultimate control of the pest will be through the use of low temperatures and freshwater.

CAUSES OF MORTALITY OF OYSTERS—In Apalachicola Bay oysters are decreasing in size and numbers. As long as 1893-1895 Swift (1897) recorded similar trouble and mentioned over-fishing, freshets, freezes, and hurricanes as contributing causes. The same obstacles to successful oystering obtain today. In addition to over-exploitation by man and decimation by extreme variations in environment, there are many living organisms that help to depopulate oyster beds. Some of these compete with oysters for space and food—algae, barnacles, mussels, sponges. There are enemies which continually attack oysters—bacteria, ciliates (Orton 1924), boring sponges, starfishes, boring clams, predaceous gastropods, crabs, fishes, birds and mammals. Not all of these are of apparent significance on the Florida coast. Oyster larvae are known to be eaten by ctenophores, worms, barnacles, copepods, mussels, clams, adult oysters, and tunicates (Nelson 1915, 1921). There are internal parasites which live within the soft bodies of oysters—spirochaetes, sporozoans, trematodes. There are many animals continually or intermittently present on oyster beds. When man has not collected oysters these tend to keep the population within the usual limits. When there has been over-fishing and destruction by culling, tonging, or dredging, these may more easily destroy weakened oysters and cause such mortality that bars become commercially unproductive. Polyclads, particularly the species known as the oyster "leech," in Florida are perhaps never the sole cause of heavy mortality on Florida oyster beds. They flourish and increase when there has been a prolonged drought and the water on the oyster beds becomes salty enough (S: 15) to permit them to reproduce. When they attack oysters they may be assisted by other organisms or physical factors which weaken, open, or kill oysters and thus render them easy to attack. High mortality on an oyster bed is probably never due to one single cause, but to a number of contributing unfavorable circumstances. This statement is not an attempt to whitewash the oyster "leech." The soft, flat, sneaking, slippery, hungry little

worm is a dark villain on oyster bars, and at times when circumstances make a favorable season does much damage.

SUMMARY

1. *Stylochus inimicus* Palombi has for many years been an enemy of oysters along the coast of Florida and at times abundant enough to constitute a serious pest.

2. Stylochus is a polyclad worm but is commonly known as the oyster "leech" in Florida.

3. The anatomy is described.

4. A single Stylochus may lay as many as 21970 eggs in less than a month. At summer temperatures (28°C. ±) these develop into a pelagic, ciliated larva in about eleven days. Stylochi usually brood their clutches of eggs until they hatch.

5. Stylochus grows rapidly and probably becomes sexually mature in less that two months under favorable conditions. It probably may live for as long as a year.

6. Stylochus does not crawl about when temperatures are below 12°C. and above 34°C. It crawls at a rate of about 40 mm. per second at 25°C. Stylochus dies below 0°C. and at 42°C. *Eustylochus,* a species also found on oyster beds, lives for hours at —2°C. and dies quicky at 39°C.

7. Eggs increase in diameter when placed in hypo- and hyper-tonic salt solutions because of the unusual osmotic pressure, caused in the first case by the low concentration of the dissolved salts in the surrounding medium and in the second case because of the low activity coefficients of the dissolved salts in higher concentrations.

8. Stylochus can live for days in very low concentrations of dissolved oxygen. At 26.5°C. an individual uses about 0.1 cc. of oxygen per gram of body weight per hour. When Stylochi were kept in closed containers progressively less oxygen was used each day, but all the oxygen present was not used up while animals were alive.

9. Exposed in dry dishes to air of 72-77% humidity Stylochi lived eight hours in open dishes and fifteen hours in covered dishes at 25.2 to 26.5°C. They lived several days in pails of shells without water. Stylochi recovered after losing 55% of body weight by desiccation.

10. Stylochus can live in salinities as low as 6 0/00, but does not lay eggs in concentrations below 15 0/00. Eustylochus tolerates lower salinities (0.6 0/00) than Stylochus. Larvae are less able to tolerate low salinities than adults.

11. The toleration of Stylochus for various dilutions of solutions of 25 different chemicals in sea water was studied. None of the substances gave promise as an agent for control measures.

12. Stylochus feeds largely on oysters. It will also eat barnacles and certain snails but refuses fish, shrimp, and most species of snails. It will enter and devour living oysters.

13. In Apalachicola Bay Stylochus was generally most abundant where oysters grew in water of relatively high salinity. Data for fifteen stations where monthly observations were made for a year are presented.

14. Stylochus will creep into a living oyster, which usually tries to shut off the intruder by building a partition. Sometimes worms are thus covered over and buried in the shell.

15. Many species of plants and animals are associated with oysters on the beds in Apalachicola Bay. A list of those identified is given.

16. *Stylochus inimicus* is a predator, not a parasite, on oysters.

17. Stylochus tolerates poisonous chemicals and low oxygen concentrations, but is susceptible to low temperatures and fresh water. Control measures should perhaps take cognizance of these facts.

18. When oysters die in numbers on beds probably several factors contribute to cause the mortality. The oyster "leech" may kill oysters but probably rarely, if ever, is the sole "cause" of the extermination of oysters in a particular locality.

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